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Mechanisms of ecosystem stability for kelp beds in urban environments

By
Simon E Reeves
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UNIVERSITY *of*
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- (ii) The work contained in this thesis, except where otherwise acknowledged, is the result of my own investigations.
- (iii) Due acknowledgement has been made in the text to all other material used
- (iv) The thesis is less than 100,000 words in length, exclusive of tables, maps, bibliographies and appendices.

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Statement of Co-Authorship

The following people and institutions contributed to the publication of work undertaken as part of this thesis:

Candidate: **Simon Reeves** – University of Tasmania, Institute of Marine and Antarctic Studies

Author 2: **Nina Kriegisch** – University of Tasmania, Institute of Marine and Antarctic Studies

Author 3: **Dr Scott Ling** (Supervisor) – University of Tasmania, Institute of Marine and Antarctic Studies

Author 4: **Prof. Craig Johnson** (Supervisor) – University of Tasmania, Institute of Marine and Antarctic Studies

Author details and their roles:

Chapter 2: Recovery potential of urban kelp beds is determined more by reef state than sediment load

Candidate was the primary author and contributed 75% to the planning, execution and preparation of the research project and subsequent paper. Authors 2, 3 and 4 assisted in the collection, analysis and interpretation of the research data, and writing of the chapter and subsequent paper by critically revising the paper.

Chapter 3: Reduced resistance to sediment-trapping turfs with decline of native kelp and establishment of an exotic kelp

Candidate was the primary author and contributed 75% to the planning, execution and preparation of the research project and subsequent paper. Authors 2, 3 and 4 assisted in the collection, analysis and interpretation of the research data, and writing of the chapter and subsequent paper by critically revising the paper.

Chapter 4: Spatially-variable development of sediment-trapping turfs under elevated nutrients, sediment, and canopy disturbance correlates with canopy community composition

Candidate was the primary author and contributed 75% to the planning, execution and preparation of the research project and subsequent paper. Authors 2, 3 and 4 assisted in the collection, analysis and interpretation of the research data, and writing of the chapter and subsequent paper by critically revising the paper.

Chapter 5: Kelp bed edges define vulnerability to overgrazing, invasion and fragmentation to a turf-dominated state.

Candidate was the primary author and contributed 80% to the planning, execution and preparation of the research project and subsequent paper. Authors 2, 3 and 4 assisted in the

collection, analysis and interpretation of the research data, and writing of the chapter and subsequent paper by critically revising the paper.

We the undersigned agree with the above stated "proportion of work undertaken" for each of the above published (or submitted) peer-reviewed manuscripts contributing to this thesis:

Signed: Candidate ____

Author 2 _

Author 3 _

Author 4 _

Date: 20/7/18

ABSTRACT

Ecologists have long been interested in determining the role biotic relationships play in natural systems. Even Darwin envisioned natural systems as "bound together by a web of complex relations", noting how "complex and unexpected are the checks and relations between organic beings" (On the Origin of Species, 1859, pp 81-83). Any event or phenomenon that alters the implicit balance in the web of interactions, to any degree, can potentially facilitate a re-organisation in structure that can lead to a wholesale change to the stability of a natural system. As a result of the increasing diversity and intensity of anthropogenic stressors on ecosystems, previously well-understood biotic interactions and emergent ecological functions are being altered, requiring a reappraisal of their effects. A key challenge lies in understanding whether, and how continuing anthropogenic change alters the relative importance of biotic interactions in determining community dynamics, or whether it creates entirely novel interactions, that modify patterns in the distribution and abundance of species at the scale of landscapes.

Along temperate coasts worldwide, shallow sub-tidal reefs are usually dominated by canopy-forming large brown alga, commonly referred to as kelp. These kelps are important foundation species supporting high production, providing habitat for many associated species, and delivering numerous ecosystem services valued in the range of billions of dollars annually. There are four classes of events well recognised to influence the nature of important biotic interactions and result in considerable alteration to shallow temperate reef ecosystems: 1) depletion or 2) increase of a foundation species, 3) addition of non-native species, and 4) the addition and interaction of multiple direct human-stressors.

The kelp *Ecklonia radiata* is arguably the single most important foundation species on southern Australian sub-tidal reefs. This thesis examines the dynamics of this species on rocky reefs in Port Phillip Bay adjacent to the city of Melbourne (Victoria, Australia). In **Chapter 2**, I examine how herbivory and sedimentation influence survival at different life-history stages of this species, and the impact of herbivory and sedimentation on the capacity of kelp beds to recover from depletion of foundation species. I identify evidence of critical bottlenecks in the kelp's life-history which act to reduce its capacity for recovery (thus reducing kelp bed resilience) due to altered strengths of competitive interactions. **Chapter 3** builds on the understanding that *E. radiata* plays a key role in structuring the benthos on Australian sub-tidal reefs and examines whether an invasive kelp (*Undaria pinnatifida*) can fulfill a similar ecological function, concluding that the invasive species cannot be a functional equivalent of the native kelp. **Chapter 3** also shows that sea urchin (*Heliocidaris erythrogramma*) grazing is leading to native kelp bed (*E. radiata*) decline in Port Phillip Bay, facilitating dominance by turf algae. Even though invasive *U. pinnatifida* establishes once the native kelp is disturbed, the ecological function performed by the exotic species in clearing away turf is weaker than that of *E. radiata*. **Chapter 4** examines the influence of multiple urban stressors – sediments and nutrients – on the resilience and resistance capacity of kelp beds. This multifactorial field experiment over 14 months showed that the response to elevated loadings of sediments and nutrients were context-dependent, dependent on the local complement of algal taxa. **Chapter 5** combines the mechanistic understanding of drivers affecting kelp bed resilience and resistance (derived from chapters 2-4) to explain patterns of loss and fragmentation of kelp bed patches at the reefscape (100 m scale). Specifically, loss and fragmentation of kelp beds is driven by urchin overgrazing at kelp bed edges, which drives a rapid increase in the ratio between perimeter (edge) and area (interior) of kelp

patches. Urchin overgrazing at the edge of kelp patches causes significant flow-on effects including breakdown of kelp recruitment, increased invasibility of non-native kelp, and development of dense turfs that inhibit kelp recruitment.

The combined results from this intensive field research highlights the importance of kelp itself for maintaining strong intrinsic and extrinsic interactions, through positive feedbacks that result in a system that is both resistant and resilient. Yet kelp is still being lost, which is fundamentally driven by high densities of the sea urchin *H. erythrogramma* in this temperate southern Australian reef system. The interaction between nutrient enrichment and loss of kelps via urchin grazing, shifts the system to a state dominated by opportunistic algae such as turfing species and *U. pinnatifida*. Moreover, once the kelp is lost and the system becomes dominated by these other species – particularly turf algae – it appears difficult for the kelp to recover, suggesting a strong hysteresis in the system. The suite of field experiments and surveys defining this thesis span multiple-spatial scales (from sub-metre to 10s of kilometres), include multiple stressors of urbanisation, and consider multiple life-history stages to build a comprehensive understanding of management actions available to minimise loss of native kelp beds and maximise the recovery potential of kelp beds under highly urbanised regimes. These include removal of urchin biomass, kelp bed restoration, and conservation efforts focused on maintaining diverse functional groups of algae to contribute to local species pools. These management actions can work in concert to maintain stability of this essential ecosystem that supports important services to human society.

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Lastly, to the fascination that sparked this journey, from the five-year-old spellbound by the ocean and its denizens to the present, a fascination I feel is perfectly captured by the following passage by Gavin Maxwell in *A Ring of Bright Water*.

“There is perpetual mystery and excitement in living on the seashore, which is in part a return to childhood and in part because for all of us the sea’s edge remains the edge of the unknown; the child sees the bright shells, the vivid weeds and red sea-anemones of the rock pools with wonder and with the child’s eye for the minutiae; the adult who retains wonder brings to his gaze some partial knowledge which can increase it, and he brings, too, the eye of association and of symbolism, so that at the edge of the ocean he stands at the brink of his own unconscious”.

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CHAPTER 1: General Introduction

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Many of the world's major urban centres have developed on large estuaries or embayments. Historically, the ability to exploit the land-sea interface has been an essential part of a nation's capacity to gain social and economic wealth and prosperity (Lotze et al. 2006; Gillies et al. 2015). However, this has not come without a cost; centuries of overexploitation, coastal engineering and related habitat transformation and pollution have precipitated an ongoing loss of biodiversity and continuing erosion of coastal ecological resilience (Lotze et al. 2006). In Australia, some 29% of estuaries are considered 'modified' (Gillies et al. 2015), and only 15% of coastlines in Europe are in 'good' condition (Airoldi and Beck 2007). With 75% of the world's population expected to reside in coastal areas by 2025, the continued loss of coastal ecological resilience is of increasing concern (Kennish 2002; Airoldi and Beck 2007; Stuart-Smith et al. 2015).

Erosion of ecological stability

Ecological stability can be viewed as the ability of a system to cope with disturbances and stressors. Disturbances are defined as events/phenomena that remove biomass either total (mortality, dislodgement or forced emigration) or partial (erosion, grazing or predation) (Grime 1977; Chapman and Johnson 1990). Stressors are defined as external constraints which limit production such as resource limitation or environmental conditions at extremes of physiological tolerances (Grime 1977; Chapman and Johnson 1990) and include the possibility of community re-organisation to retain essentially the same function, but not necessarily the same complement of taxa (Folke et al. 2004). The concepts of resistance and resilience are often merged in the concept of ecological stability (Holling 1973; Westman 1978; Aronson et al. 1993; Folke et al. 2004), however, there is value in viewing them as

sibling concepts – closely related but independently measurable (Lake 2013; Nimmo et al. 2015; Connell et al. 2016). An ecologically stable system is thought to be i) resistant – having the capacity to withstand a disturbance/stressor, and ii) resilient – having the capacity to recover from a disturbance/stressor that causes a change in community structure, usually through species losses resulting in shifts in relative abundance (Connell and Sousa 1983; Pimm 1984; Tilman and Downing 1996; Lake 2013; Nimmo et al. 2015).

In many cases, erosion of ecological stability stems from the combined effects of multiple anthropogenic stressors at local (e.g. nutrient enrichment, over-harvesting and increased sedimentation) and global (e.g. warming and acidification) scales (Folke et al. 2004; Strain et al. 2015; Stuart-Smith et al. 2015). These stressors can alter the strength and types of ecological interactions (i.e. competition, facilitation, and predation) to reduce stability (Crain et al. 2008; Gunderson et al. 2016), and in some cases precipitate shifts to alternative states (Scheffer et al. 2001; Folke et al. 2004; Strain et al. 2014; Ling et al. 2015). Examples of switches to contrasting states have been reported from other marine ecotypes such as coral reefs (Mumby et al. 2006; Hughes et al. 2007; Fung et al. 2011) and kelp forests. In the case of kelp communities, the shift can be from kelp dominance to dominance by sea urchins (Lawrence 1975; Steneck et al. 2002; Konar and Estes 2003; Ling et al. 2015) or algal turf-forming species (Airoldi and Cinelli 1997; Gorgula and Connell 2004; Perkol-Finkel and Airoldi 2010). Importantly, once a system shifts to an alternative state, reducing the drivers of the change to levels that previously supported kelp will not necessarily result in kelp recovery. For this reason, it is essential to understand the mechanisms that cause and prevent phase shifts from desirable ecosystem states. This research is a central focus for ecologists, and knowledge of the emergent dynamics of ecosystems should underpin management decisions

and policy development.

Temperate rocky reefs

Typically, along temperate coasts worldwide, shallow sub-tidal reefs are dominated by large brown alga of the orders Laminariales and Fucooides, commonly referred to as kelps (Dayton 1985, Steneck and Johnson 2014). These canopy-forming brown algae are vital foundation species (*sensu* Dayton 1972), occupying close to half of the world's marine ecoregions (Steneck et al. 2002; Spalding et al. 2007; Steneck and Johnson 2014; Krumhansl et al. 2016). Kelps provide three-dimensional habitat structure, standing biomass, and food for a diverse range of associated species (Dayton 1985; Ling 2008; Christie et al. 2009 and Coleman et al. 2007). As biogenic habitats, kelp beds also influence local environmental factors such as water motion (Eckman et al. 1989; Jackson 1997; Wernberg et al. 2005), light (Kennelly 1989; Connell 2003; Wernberg et al. 2005), sediment accumulation (Eckman et al. 1989; Wernberg et al. 2005), and pH (Hofmann et al. 2011; Roleda et al. 2015; Britton et al. 2016). For these reasons, kelp beds support numerous ecosystem services, including commercial fisheries, nutrient cycling, and shoreline protection, valued in the range of billions of dollars annually (Smale et al. 2013; Bennett et al. 2016). Consequently, change in the abundance of kelps has significant consequences for ecosystem health and the provision of services.

The 'natural' state on shallow temperate rocky reefs is thought to be of kelps coexisting with patches devoid of kelp that are dominated by small foliose and filamentous algae (Thomson et al. 2012; Marzinelli et al. 2015). This natural state of patchiness within a canopy can be maintained by disturbance from waves and/or small-scale invertebrate or fish grazing, which removes plants and creates open areas (Dayton 1985). It is likely that kelp-free

patches always occur at some scale, but those created by natural physical factors tend to be relatively small and transient (Steneck et al. 2002). Such open areas are often colonised by turf-forming algae, which, due to its vegetative mode of reproduction, can often out-compete other larger algae, thus slowing or even preventing the recovery of canopies. Conversely, kelps inhibit the growth and colonisation of turf-forming algae through abrasion by algal blades scouring the benthos, and restricting light intensity via shading (Velimirov and Griffiths 1979; Duggins et al. 1990; Irving and Connell 2006). Under natural regimes of disturbance, these interactions act to stabilise the presence of alternative canopy and open-area patches (Kennelly 1987a; Johnson and Mann 1988; Thomson et al. 2012) within a kelp bed.

Historically kelp habitats have primarily been considered highly ecologically resilient (Dayton et al. 1984; Kennelly 1987b; Kennelly 1989; Dayton et al. 1992), but a number of recent studies have suggested that the resistance and resilience capacity of kelps to stressors and disturbances has been eroded (Ling et al. 2015; Krumhansl et al. 2016; Filbee-Dexter and Wernberg, 2018; O'brien and Schiebling 2018). Contemporary studies piecing together historical baseline information and dynamics over past decades have documented distinct reductions in cover of some macroalgal habitats (Benedetti-Cecchi et al. 2001; Eriksson 2002; Coleman et al. 2008; Connell et al. 2008), and these losses – often representing shifts in ecosystem state – have been primarily driven by two mechanisms.

The first such mechanism is the overgrazing shift from luxuriant and productive kelp beds to impoverished and persistent sea urchin barrens and is perhaps one of the best-studied ecosystem shifts on temperate rocky reefs (Steneck et al. 2002; Konar and Estes 2003; Ling et al. 2015). This shift is often associated with overfishing of sea urchin predators,

273 leading to outbreaks of grazers and destructive overgrazing of kelps (Steneck et al. 2002; Ling
274 2008; Ling et al. 2009; Ling et al. 2015).

275 The second of these mechanisms typically occurs on heavily urbanised coasts,
276 whereby kelps are displaced by ephemeral turf forming species that create a turf-sediment
277 matrix (Kennelly 1987a; Kennelly 1987b; Airoldi and Virgilio 1998; Irving and Connell 2002a;
278 Airoldi et al. 2008; Connell et al. 2008; Gorman and Connell 2009). As a consequence of the
279 turfs ability to colonise rapidly and retain space, this degraded habitat flourishes under
280 enhanced rates of sedimentation and nutrient input found on urbanised coasts (Gorgula and
281 Connell 2004). Specifically, enhanced nutrient loading enables turf growth to override grazer
282 control, and the (usually) filamentous algal morphology and rapid growth facilitate trapping
283 of sediments to produce a semi-consolidated turf-sediment matrix in which turfs proliferate
284 even under heavy deposition of sediments. In turn, the turf-sediment matrix can inhibit
285 recruitment of kelps (Kennelly 1987a; Gorman and Connell 2009). In this way, elevated urban
286 stressors can result in normally subordinate taxa (turfs) becoming dominant over kelps.
287 Significantly, the newly established habitat, whether urchin barren or turfs, is simplified and
288 represents a relatively depauperate community of reduced ecological function and service
289 that can persist for decades, if not permanently, without management or restoration
290 intervention (Folke et al. 2004; Airoldi et al. 2008; Nyström et al. 2012).

291 The ability of formerly dominant species to recover from disturbance through natural
292 recruitment is an essential process in population dynamics and landscape configurations of
293 ecosystems, especially for component species living in highly disturbed areas and subjected
294 to frequent local extinctions. For many primitive plants such as kelps, the process of
295 recruitment (i.e., the first appearance of macroscopic individuals) is quite complex and

requires the successful completion of an alternate microscopic free-living sexual stage see Fig. 1 (Reed 1990; Schiel and Foster 2006). A number of studies have shown turfs to inhibit the early-life history stages of kelp (stages a – f, Fig. 1), whether via competition for space, altering the substratum chemically, direct inhibition of settlement through the instability of the turf-sediment matrix, or via harbouring greater abundance of micro-grazers within turfs that inhibit recruitment through increased grazing pressure on kelp recruits (Kennelly 1987a; Vadas et al. 1992; Gorman and Connell 2009).

Inhibition of recruitment of the kelps *Ecklonia radiata* (Kennelly 1987a; Gorman and Connell 2009), *Macrocystis pyrifera*, and fucoids both within intertidal and sub-tidal zones (Benedetti-Cecchi and Cinelli 1992; Worm and Chapman 1998; Schiel and Lilley 2011) by turfing species has also been identified. Recovery of canopy formers following manual removal of turfs has been reported for southern Australia (Gorman and Connell 2009) and California (Reed and Foster 1984) and has been used to suggest possible mechanisms for encouraging the recovery of canopy-forming kelps. Such physical disturbance, whether by significant wave action, storms, manual removal or natural levels of herbivory, can therefore play a vital role in the establishment of kelps, turfs, or perhaps more alarmingly, invasive species, with canopy removal being a key instigator for the establishment of invasive macroalgal species (Valentine and Johnson 2003; Valentine and Johnson 2004; Valentine and Johnson 2005; Valentine et al. 2008).

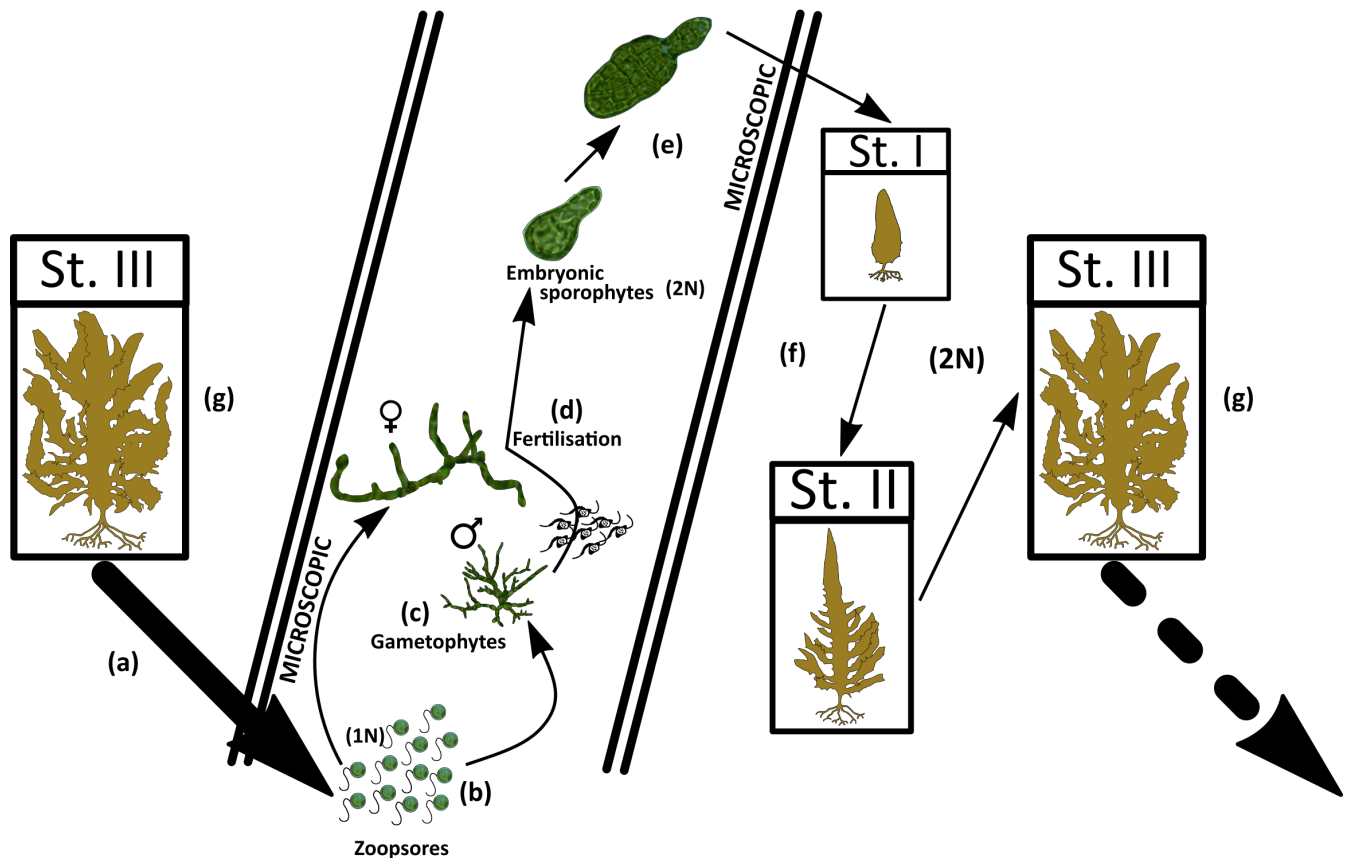


Figure 1. The life history of the laminarian *Ecklonia radiata*, a typical kelp showing heteromorphic alternation of generations (redrawn from Reed, 1990, Kirkman, 1981, Womersley, 1997 and Fig. A: <https://wernberglab.org/past-staff-students/margie-mohring/>). Kelp recruitment requires the successful completion of an alternate sexual generation, the microscopic gametophyte stage (c). Following release from the adult sporophyte (a) motile zoospores (b) settle and germinate into either male or female gametophytes (c). Gametophytes are sessile, free-living plants. When sexually mature they produce eggs or sperm, which after fertilisation (d) develop from microscopic embryonic sporophytes (e) to visible non-reproductive sporophytes (St I and St II) (f) and St III reproductive sporophytes (g). Thus, sporophyte recruits in kelps are derived from an intermediate stage and are not the same individuals as those that initially settled

It is evident that the inherent capacity of some kelp bed ecosystems to buffer change has become progressively reduced by increased intensity and frequency of both local stressors (e.g. over harvesting of apex predators [Steneck et al. 2002; Ling et al. 2015], nutrification [Worm and Lotze 2006; Falkenberg et al. 2015], and sediment inputs [Strain et al. 2014; Strain et al. 2015] and global stressors e.g. warming [Johnson et al. 2011; Smale and Wernberg 2013; Wernberg et al. 2013], and increased climatic forcing on water motion [Strain et al. 2015]). It is clear that the stability of these vital systems cannot be taken for granted (Folke et al. 2004; Hughes et al. 2005). Therefore, understanding the interactions between human-induced stressors and natural processes remains a key factor in not only managing for enhanced stability of desirable and productive ecosystems but also in identifying the circumstances in which collapsed systems may be recovered and important ecosystem services restored (Gorman and Connell 2009; Nyström et al. 2012).

An urbanised temperate reef system – Port Phillip Bay

Port Phillip Bay (PPB), Victoria, lies adjacent to Australia's second largest city and has been subject to a variety of anthropogenic impacts for more than a century. Melbourne is currently the fastest growing capital city in Australia, growing from a population of 3.5 million in 2001 to 4.16 million in 2011 (a growth rate of 1.7% p.a.; Australian Bureau of Statistics, 2012). The impacts upon PPB since colonial settlement in the mid-1800s have been considerable. Ongoing catchment alterations have led to enhanced sediment, nutrient, and pollutant inputs, there has been intense commercial and recreational fishing, and high levels of recreational and commercial boating have also contributed to the loss or degradation of habitat (e.g. Jung et al. 2011). PPB is regarded as one of the most invaded marine ecosystems in the southern hemisphere; no doubt due to its industrialised nature centred around two

busy ports, Melbourne and Geelong (Hewitt et al. 2004). One invasive species of major concern to kelp bed dynamics in PPB is the Japanese kelp *Undaria pinnatifida*, which was first observed in PPB in July 1996 (Campbell et al. 1998). However, little is known about its distribution on subtidal reef habitats across PPB, or of possible synergistic impacts between this species and other factors leading to altered reef states.

This thesis aims to examine factors affecting the ecosystem stability of kelp beds in PPB. Anecdotally, kelp beds are undergoing decline throughout much of PPB (Jung et al. 2011). While numerous studies have shown that kelps are a key foundation species capable of influencing the physical and biological environment of rocky reefs (Fowler-Walker et al. 2006; Irving et al. 2002a, 2002b; Kendrick et al. 1999; Russell et al. 2005; Smale et al. 2011; Toohey et al. 2004; Wernberg et al. 2005), most studies have been undertaken on ‘pristine’ non-urban open-coast sites (Ling 2008; Bennett and Wernberg 2014; Flukes et al. 2014), or using simplified experimental communities (Irving and Connell 2002b; Connell 2005; Strain et al. 2015) including mesocosms (Bokn et al. 2003; Falkenberg et al. 2015; Ghedini et al. 2015). Additionally, many of these study systems have rarely experienced the high intensity and/or frequency of urban stressors as experienced by reefs within PPB. While a number of studies have examined the isolated impacts of physical disturbance (Kennelly 1987b; Toohey et al. 2007), or sediments (Airoldi 2003; Balata et al. 2007; Kawamata et al. 2012), or nutrients (Irving and Connell 2002a; Irving and Connell 2002b; Gorgula and Connell 2004; Russell and Connell 2005; Russell and Connell 2007; Valdivia et al. 2008; Gorman et al. 2009), or invasive kelps (Casas et al. 2004; Valentine and Johnson 2004; South and Thomsen 2016) on kelp bed communities, none have explicitly examined possible interacting effects (synergistic or otherwise) of combinations of these three factors on the dynamics of kelp beds. In addition,

the sea urchin *Heliocidaris erythrogramma* is a potential driver of kelp bed dynamics in PPB since it forms widespread barrens in many regions of PPB (Constable 1990; Carnell and Keough 2016; Kriegisch et al. 2016) and has been shown to create and maintain barrens at other southeast Australian localities (Ling et al. 2010, Wright et al. 2005, Johnson et al. 2004). Overall, a mechanistic understanding of these dynamics is essential to identify key drivers of kelp loss, and to outline clear management actions to minimise further loss of native kelp beds and maximise the potential for recovery of native kelp beds under highly urbanised regimes.

Thesis outline

An ecological system is a web of trophic, competitive, and various kinds of mutualistic interactions, covering positive, negative, and neutral effects. Any event or phenomenon that alters the implicit quasi-equilibrium in a web of interactions can facilitate a re-organisation in structure that could represent a wholesale change to the system (Holling 1973; Folke et al. 2004). For temperate subtidal kelp-dominated reefs, four kinds of events can result in considerable alterations to community structure: 1) depletion or 2) increase of a foundation species, 3) addition of non-native species, and 4) the addition and interaction of multiple direct human-stressors. In the following chapters of this thesis, I investigate how these events play-out on the temperate reefs of PPB. In **Chapter 2**, I examine how herbivory and sedimentation influence survival at different life-history stages of the primary foundation species on PPB reefs (*Ecklonia radiata*) and the impact that these stressors have on the capacity for this kelp to recover following depletion. In **Chapter 3**, I investigate how removal of this foundation species influences the structure of temperate rocky reef understory

397 communities, and whether, following loss of the native kelp, an invasive kelp species
398 (*Undaria pinnatifida*) can fulfil the same ecological function. **Chapter 4** further examines the
399 influence of multiple urban stressors (sediments and nutrients) on the resilience and
400 resistance capacity of kelp beds through a multifactorial experiment. **Chapter 5** combines
401 mechanistic understanding of drivers affecting kelp bed resilience and resistance derived
402 from chapters two, three and four to explain patterns of loss and fragmentation of kelp beds
403 at the reefscape scale. Lastly, in **Chapter 6** (“General Discussion”) I attempt to integrate the
404 various interacting processes explored through this project into a cohesive conceptual model
405 of the dynamics of shallow subtidal reefs in PPB, and I discusses the implications of the
406 findings for the effective management of these reefs including restoration of kelp beds.

407 Readers should note that this thesis is prepared as a set of stand-alone papers for
408 submission to peer-reviewed journals. It is therefore inevitable that there is overlap in
409 material between chapters, particularly in the Introduction sections.

410

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729 CHAPTER 2: Recovery potential of urban kelp
730 beds is determined more by reef state than
731 sediment load

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Abstract

The capacity for a kelp bed to recover and persist following a perturbation is governed by interactions between external drivers (both biotic and abiotic) and the biological characteristics of taxa comprising local species pools available to colonise space. I undertook field-observations (spanning 18-24 months) of kelp (*Ecklonia radiata*) dynamics, sediment deposition and sea urchin (*Heliocidaris erythrogramma*) biomass. These field observations were combined with field experiments utilising kelp transplants and settlement panels with manipulations of urchin biomass and sediment load within two habitats, across four sites to identify 'bottlenecks' in the recovery potential of kelp beds in Australia's largest urbanised embayment, Port Phillip Bay (PPB), Victoria. Kelp spore production per unit area of sorus was high, but variable per unit area of seafloor due to variation in sporophyte density. High propagule supply did not necessarily produce large numbers of kelp recruits, with sites with high propagule supply often displaying low recruitment. Recovery potential of kelp beds was highly site and habitat specific with kelp bed recovery only apparent at one site and reduced at other sites due to the predominance of turfs and opportunistic taxa such as *Ulvaceae spp.* Sediment deposition was high and variable in PPB and an experimental loading of two times ambient sediment load had little effect on the development of algal communities. Survival of established *E. radiata* was reduced by sea urchin grazing, and on urchin barrens, grazing of early kelp recruits was particularly severe. Experimental reduction of urchin biomass on barrens habitat by 50%, increased survival of *E. radiata* to that observed in kelp beds. Overall, I identified that altered strengths of algal-algal competition results in kelps being outcompeted in their early-life history stages, and high biomass of urchins acts as the key bottleneck for kelp populations due to overgrazing of sporophytes. These findings suggest continued loss of kelp bed resilience unless mitigation efforts can maintain stability of kelp

784 beds through 1) maintaining high propagule pressure, 2) reducing factors that confer
785 competitive advantage to the turfs, and 3) reducing urchin biomass to increase the survival of
786 recruiting sporophytes.

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Introduction

Natural systems are rarely static, and communities of organisms are continuously being altered by physical and biological perturbations (Paine et al. 1998). The capacity of a community to persist in some form of quasi-equilibrium without switching to a distinctly different alternative state following perturbations defines the stability of a system (Holling 1973; Ghedini et al. 2015). Persistence of a dominant species or suite of taxa over several life cycles indicates a stable system (Connell & Sousa 1983). However, the factors defining the ability of a particular community configuration to persist reflects both the ability of a system to recover from disturbances (resilience) and capacity to withstand other pressures and perturbations through their growth and reproduction (resistance). The underlying processes are influenced by a multitude of extrinsic and intrinsic factors, such as the nature and scale of the perturbation, physical environmental characteristics (e.g. nutrients, space), nature of biological drivers (e.g. predator-prey and competition interactions, and reproductive characteristics of the space occupiers) (Grime 1977; Paine 1984; Airolidi 1998).

Many ecosystems can be characterised by the dominance of a single functional group that remains approximately stable throughout time, e.g. coral reefs (Connell 1978), tropical rainforests (Connell 1978), grasslands (Tilman et al. 2006), and temperate reefs dominated by large brown macroalgae (Dayton 1985; Steneck and Johnson 2014). The presence of these biogenic habitat-forming species influences the surrounding environment, usually facilitating their own recruitment and conferring a competitive advantage over other species that may otherwise inhibit the foundation species. Additionally, habitat-formers create a local environment for associated species and are critical for the provision of services to both humans and nature (Ellison et al. 2005; Bennett et al. 2016). However, as human activities

increase and continue to modify abiotic and biotic conditions, there is evidence that these pressures can alter the strength and nature of the ecological interactions that underlie the stability of marine benthic communities (Crain et al. 2008; Gunderson et al. 2016) increasing likelihood of shifts in ecological state (Folke et al. 2004; Conversi et al. 2015; Ling et al. 2015)

The shift on temperate rocky reefs from luxuriant and productive habitat-forming large brown alga (of the orders Laminariales, Desmarestiales, and Fucales, commonly known as kelps; Dayton 1985; Steneck and Johnson, 2004) to impoverished and persistent sea urchin barrens is perhaps one of the best studied marine ecosystem shifts (Lawrence 1975; Steneck et al. 2002; Konar and Estes 2003; Ling et al. 2015). The overgrazed reefs (barrens) are structurally simple and impoverished, with altered ecological function that can persist for decades, if not permanently, without management or restoration (Estes and Duggins 1995; Steneck et al. 2002; Ling et al. 2015). Notably, the persistence of degraded states can occur due to establishment of competitive or trophic feedbacks that prevent re-establishment of the former state. Thus, critical for recovery of kelp beds on urchin barrens is not only a reduction in grazing intensity, but also supply and fertilisation of kelp propagules, and growth and survival of sporelings to produce adult sporophytes. However, altered conditions on degraded reefs may feedback to prevent re-establishment of kelp beds, even after the mechanism of initial decline is removed or has subsided. This is an increasingly likely outcome on urban coasts where the impacts of multiple anthropogenic stressors combine to maintain non-kelp bed regimes (Strain et al. 2014; Strain et al. 2015).

Deposited sediments can negatively impact survival and recruitment of kelps (Perkol-Finkel and Airolidi 2010; Watanabe et al. 2016), and act as a key driver of reef communities

(Airoidi 2003). Sediments can influence algal communities and other sessile organisms on reefs both directly, through processes such as scour/abrasion, burial of individuals, and inhibition of propagule settlement or development (Airoidi 2003; Watanabe et al. 2016), and indirectly through benefitting more sediment tolerant taxa such as turf and ephemeral algae (Airoidi 1998; Airoidi 2000; Connell et al. 2014). As sediment input to coastal environments increases as a result of changes in land use, coastal construction, beach erosion and nourishment and dredging of shipping channels (Airoidi 2003; Strain et al. 2015), understanding the effects of sedimentation on reef communities is becoming increasingly important for managing their resilience and resistance.

This study aimed to examine the recovery potential of degraded urban kelp beds by examining key life-history stages of the habitat-forming kelp *Ecklonia radiata*. I used field observations and manipulative field-experiments within kelp beds and on sea urchin barrens at four sites within an urban embayment to examine putative life-history bottlenecks in recovery of *E. radiata* at multiple life-stages, including 1) pre-settlement (i.e. propagule supply); 2) recruitment; and 3) post-settlement processes. I assessed survival of three age-classes, and net growth of adult sporophytes. I examined the hypothesis that the habitat characteristics in which these life-history phases occur, and the nature of stressors, will influence patterns of settlement, post-settlement survival, and ultimately recovery potential of *E. radiata*. The focus was on the effect of elevated sediments on patterns of recruitment of algae in two habitats – urchin barrens and kelp beds – and the effect of elevated urchin biomass on post-settlement survival of the kelp.

Materials and Methods

Site description

Port Phillip Bay (PPB) is Australia's largest (1,930 km²) urbanised embayment (Fig. 1). The shores of PPB house Australia's second largest, but fastest growing metropolitan population (Australian Bureau of Statistics 2012). Following initial scoping of PPB reefs based on 27 km of manta towed diver observations (January 2012), surveys and experiments were undertaken at four reef sites that were purposefully chosen to represent the typical reef habitats of each of the four biogeographically distinct regions of PPB (after Johnson et al 2015). All reef sites were located at a standard depth of ~3 m and were positioned to represent the approximate centroids of the available reef habitat across the four biogeographical regions of PPB, viz. the west, north, southeast, and southwest (Fig. 1).

Subtidal reefs of the western and northern regions are composed of basaltic rock (Bowler 1966). The western reefs (S 38°1'35.742", E144°34'58.5516") are composed of mixed rocky slabs and boulders interspersed with sand patches (10¹-10² m²). This region is dominated by the sea urchin *Heliocidaris erythrogramma* (Valenciennes, 1846; Family: Echinometridae), which overgrazes macroalgae to form and maintain sea urchin barrens that are associated with high cover of bare-rock and/or encrusting corallines, but very low macroalgal cover and no kelps. Reefs in the northern region (S 37° 52' 10.5564", E 144° 53' 36.4884") are predominantly composed of boulder and cobble reef interspersed by small (10¹ m²) patches of sand. The reef community in this region is composed of small remnant beds of the native kelp *Ecklonia radiata* [(C. Agardh) J. Agardh 1848, Family: Lessoniaceae] patchily distributed among *H. erythrogramma* barrens which dominate and are associated

with high cover of bare-rock and/or corallines frequently covered by mat-forming turfing algae.

The southeastern and southwestern reefs of PPB are composed of sandstone (Bowler 1966).

The southeastern reef (38°12'47.8836", E 145°1'56.517") is comprised of mixed boulder and

pebble reef interspersed with flat rock and small (1-5 m) patches of gravel and sand. The

macroalgal community is rich, and the cover is high (see Appendix 1) from the shore to 4.5 m

depth where *H. erythrogramma* barrens dominate down to the sand flat at 6.5 m depth. In

the southwest (S 38° 8'56.69", E 144°43'26.37"), the reef is characterised by large boulders

and pebble conglomerate reef interspersed by sand patches (10¹ m²). Here sea urchin

barrens do occur, but not as extensively as in other regions. Macroalgal cover in the

southwest is primarily thick *E. radiata* beds interspersed with Fucales species, with species

richness of canopy-formers similar to the southeast. I assessed the regional differences in

macroalgal communities to define the "background" community before experimentation; see

appendices at the end of the chapter for survey methodology, statistical methods, analysis,

and tables of regional abundance of macroalgae in each habitat (see Appendices 1, 2 & 3). A

two-way PERMANOVA for each habitat (kelp bed and urchin barren) showed that the

macroalgal communities surveyed in all regions in each habitat were different (urchin barren:

Pseudo-F_{3,174}=25.25, P(perm) < 0.0001; kelp bed: Pseudo-F_{2,124}=39.47, P(perm) < 0.0001) see

supplementary material for methods and detailed results (see Appendix 4).

Table 1. (a) Ambient sediment deposition (mean $\text{g m}^{-2}\text{d}^{-1} \pm \text{SE}$) and sediment load (mean $\text{g m}^{-2} \pm \text{SE}$) experienced throughout a 31 month period between May 2012 and November 2014 at each experimental site and habitat. 'Treatment' refers to the deposition rate and load applied to settlement panels. (b) Ambient urchin density and biomass (mean $\pm \text{SE}$) in each site and habitat, and the density and biomass in urchin reduction treatments as part of the transplant experiment.

a. Sediment deposition

Site	Habitat	Ambient		Sediment +	
		Deposition ($\text{g m}^{-2}\text{d}^{-1}$)	Load g m^{-2}	Deposition ($\text{g m}^{-2}\text{d}^{-1}$)	g m^{-2}
west	-	240.1 \pm 66.2	10841.0	516.2	21682.1
north	Kelp	947.9 \pm 326.9	34813.4	1657.8	69626.8
	Barren	329.8 \pm 64.7	13849.5	659.5	27699.0
southeast	Kelp	1010.9 \pm 553.2	42457.0	2021.8	84913.9
	Barren	540.8 \pm 209.8	24576.3	1170.3	49152.6
southwest	Kelp	321.3 \pm 135.9	13494.2	642.6	26988.4
	Barren	286.7 \pm 72.48	12041.0	573.4	24082.0

(b) *Heliocidaris erythrogramma* abundance

Site	Habitat	Ambient		Reduced	
		Density (m^{-2})	Biomass density (g m^{-2})	Density (m^{-2})	Biomass density (g m^{-2})
west	-	19.8 \pm 1.1	420.1 \pm 23.1	6.8 \pm 0.8	145.6 \pm 16.7
north	Kelp	3.9 \pm 0.7	146.8 \pm 25.6	-	-
	Barren	3.9 \pm 0.28	145.8 \pm 10.8	0.9 \pm 1.2	35.7 \pm 46.3
southeast	Kelp	2.3 \pm 0.4	295.4 \pm 54.4	-	-
	Barren	3.8 \pm 0.2	492.3 \pm 31.3	1.6 \pm 0.2	199.1 \pm 23.3
southwest	Kelp	2.55 \pm 0.8	194.6 \pm 57.6	-	-
	Barren	4.65 \pm 0.4	355.98 \pm 31.1	0.65 \pm 0.2	49.6 \pm 12.5

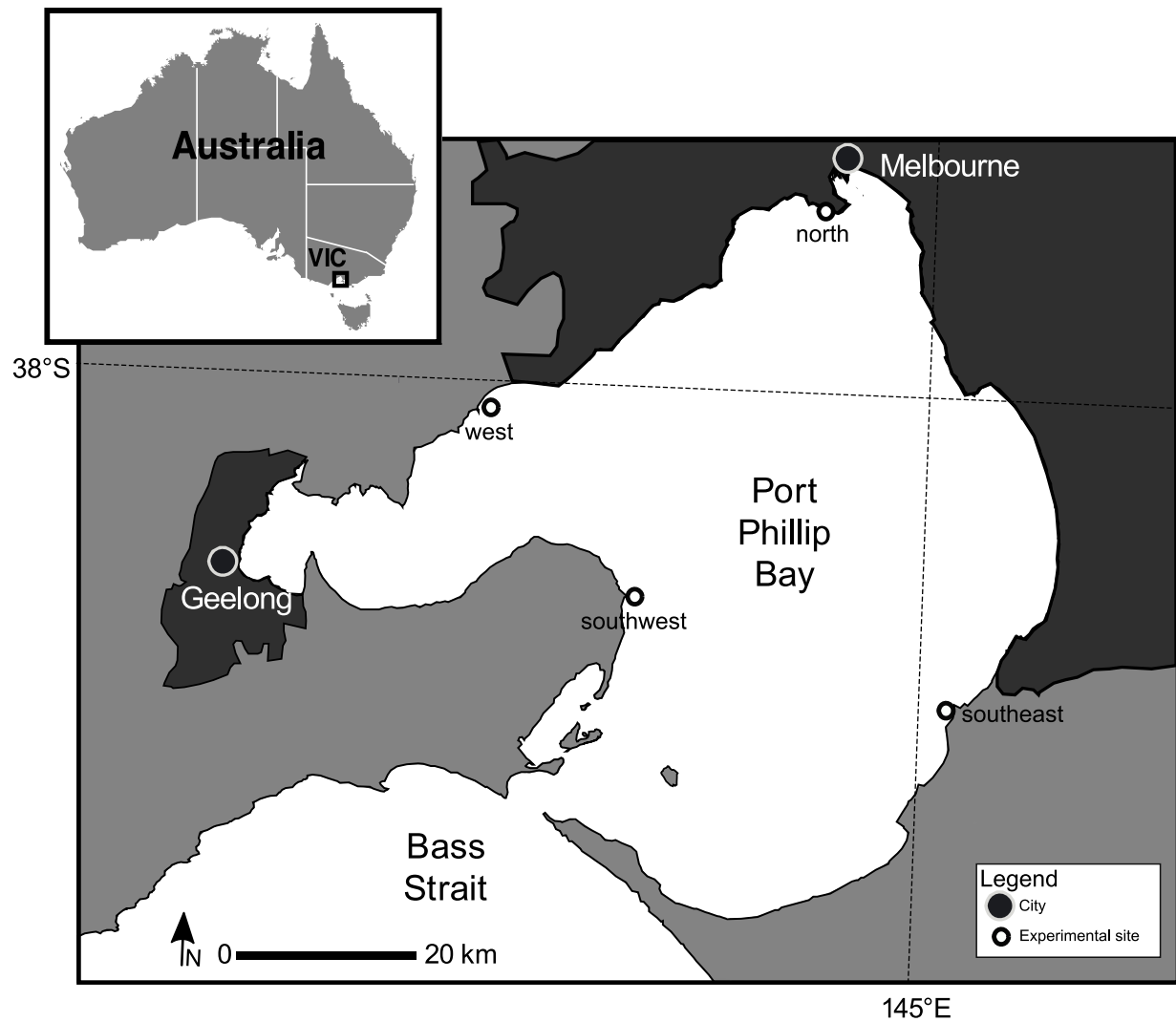


Figure 1. Map of Port Phillip Bay, an urbanised embayment in southeastern Australia. Major cities (large symbols, bounded in white) and the study sites (small white symbol, bounded in black) are shown, urbanised extent of cities is indicated by dark grey polygons.

957 *Assessing Ecklonia radiata dynamics*

958

959 *Life-stage classification*

960 Three 1 x 1 m fixed plots, spaced 25 m apart within kelp beds were surveyed monthly over 23
 961 months spanning November 2012 (west and southeast) and February 2013 (north and
 962 southwest) to October (2014) to determine the temporal dynamics of *Ecklonia radiata*.
 963 Following Kirkman (1981), I classified *E. radiata* individuals into three stages to differentiate
 964 between the morphological forms and maturity of *E. radiata* sporophytes. Stage I thalli
 965 (length 4.1 – 212 mm; wet weight 0.001 – 4.22 g) are teardrop to oblong in shape with no
 966 lateral branches. Older *E. radiata* are characterised by one central lamina lined on either side
 967 by lateral branches (laterals) (Mann and Kirkman 1981). From the simple shape of Stage I
 968 thalli small protuberances on the lateral edges of the central lamina develop into simple but
 969 distinct laterals, and the thallus is classed as Stage II (length 5.4 – 308 mm; wet weight 0.79 –
 970 32 g). The Stage III thalli (length 72 – 879 mm; wet weight 11.09 – 486 g) have complex
 971 laterals and are the only life-stage to bear sori. The density of all stages of *E. radiata*
 972 sporophyte was assessed at all four sites monthly for ~24 months from November 2012 to
 973 November 2014.

974 For the productivity and reproductive analyses, two individual Stage III *E. radiata* were
 975 sampled adjacent to each fixed plot at each site (n=6 per site per month) for a period of 20
 976 months from March 2013 to October 2014. Prior to any analyses the hold-fast was cleaned of
 977 all associated macro-organisms and individual stipe length (*St*), total length (*Tl*), midrib
 978 length (*ML*), lamina width (*Lw*), and plant wet weight with and without the holdfast (*Tww+*
 979 and *Tww-* respectively) were recorded for each sporophyte. Post measurement algae were
 980 air dried at 80°C for 24-48 hours and dry weight recorded (*Tdw*).

981 *Productivity*

982 Here I define productivity as the gross amount of new biomass that is added to the *E. radiata*
 983 thallus by the process of photosynthesis while accounting for the amount of tissue lost by
 984 erosive processes (i.e. grazing by herbivores or sloughing of dead material from the distal
 985 ends of the plant). I use a modified version of the method of Mann and Kirkman (1981) to
 986 assess production; 2 Stage III thalli adjacent to each fixed plot were tagged, a hole was
 987 punched a set distance above the meristem at the top of the stipe, and the distance from the
 988 hole-punch to the distal tip of the lamina was also recorded (El). Due to large size variation of
 989 mature Stage III *E. radiata* between sites, two hole-punch distances were used, 100 mm in
 990 the north (mean *E. radiata* TI: 367.05 ± 87.42 mm) and southwest (mean *E. radiata* TI: 385.91
 991 ± 127.21 mm), and 50 mm in the southeast (mean *E. radiata* TI: 208.66 ± 57.59 mm). After ~ 1
 992 month (No – the number of days since initial hole-punch) the tagged thalli were hole-
 993 punched at the same distance above the meristem and collected, two length measurements
 994 were recorded: 1) the distance that the punched hole had moved (l) and 2) the distance from
 995 the initial hole-punch to the tip of the lamina (El). The growth section (i.e. the section
 996 between the two hole-punches) was dissected from the entire plant and wet and dry weights
 997 recorded ($Gs(ww)$ and $Gs(dw)$ respectively).

998 Biomass per mm (Bm) was calculated by:

$$999 \quad Bm = \frac{Gs(dw)}{Ml}$$

1000 Growth rate (G as $g\ d^{-1}$) was calculated as:

$$1001 \quad G = \frac{(l \times Bm)}{No}$$

1002 The amount of biomass lost by erosive processes (E as g d^{-1}) was calculated by:

1003
$$E = \frac{((E_i - E_f) \times Bm)}{No}$$

1004 Productivity was then calculated as growth rate minus erosion rate.

1005 *Estimating the reproductive output of Ecklonia radiata*

1006

1007 Before drying, the same tagged thalli were additionally assessed for zoospore release, and

1008 propagule pressure was calculated as the propagules per square metre of reef based on the

1009 method of Mohring et al. (2013). Because most of the sorus-tissue was located on the midrib,

1010 laterals were first trimmed away from the mid-rib, the mid-ribs were then desiccated (1-hour

1011 air drying at room temperature), the percentage of the mid-rib covered by sori determined

1012 (using point estimates with a grid of points at 10 mm spacings), and individual sori

1013 subsampled by punching consecutive discs of sorus tissue (27 mm diameter) in a line from

1014 the distal end to the base of the mid-rib. These discs were then soaked together in 50.0 ml of

1015 filtered seawater for 20 minutes. After soaking, 0.1 mL of 70 % ethanol was added to the

1016 resulting zoospore solution. The number of zoospores in two 1*1 mm (0.1 μL) grids was

1017 counted using a Neubauer counting chamber loaded with 1 ml of zoospore solution for a

1018 total of three subsamples (six 1*1 mm grids). The results were averaged and expressed as the

1019 number of zoospores released per unit area of sori sampled (i.e. total area of discs of tissue).

1020 I calculated the zoospores produced per sporophyte by multiplying the number of zoospores

1021 released by the area of sorus tissue. Propagule pressure was estimated as the mean zoospore

1022 production per sporophyte multiplied by mean sporophyte density.

1023

1024 *Estimating survival from spore to visible sporophytes*

1025 To avoid complications due to the microscopic nature of early kelp life stages, I undertook
 1026 what Schiel and Foster (2006) termed a ‘black box’ approach, whereby I correlated inputs of
 1027 spore abundance and outputs as settled visible recruits. I estimated annual propagule
 1028 pressure by integrating under propagule pressure curves for all sites by using the spline
 1029 integration method from the MESS package in R (Ekstrom 2014). Assuming a 1:1 sex ratio and
 1030 1 egg per gametophyte (Schiel and Foster 2006), and using the maximum number of Stage I
 1031 and II *E. radiata* per m² in a year as an estimate of the total number of ‘successful’ settled
 1032 recruits, I calculated estimates of proportional survival from spore to Stage 1, then from
 1033 Stage 1 to Stage II thalli for each region.

1034 *Sediment deposition on kelp-dominated and urchin barren reefs*

1035 Baffled cylindrical PVC sediment traps with an aspect ratio of 6 (height 600 mm, diameter
 1036 100 mm) were utilised to measure sediment deposition in this study. I acknowledge some
 1037 potential shortcomings of this method due to sampling inefficiencies of baffled sediment
 1038 traps in highly dynamic environments such as shallow subtidal reefs (Blomquist 1981; Baker
 1039 et al. 1988; White 1990). However, this was determined to not be an issue, and I recognised
 1040 that sediments sampled in our sediment traps may not solely represent vertical flux but also
 1041 horizontal flux. However, total load measured in this way is more useful for our purposes,
 1042 and it was outside the scope of the study to decompose sediment deposition into rates from
 1043 vertical versus horizontal flux. Additionally, White (1990) showed that baffled cylindrical
 1044 sediment traps with an aspect ratio of >5 performed with ~100% sampling efficiency in a
 1045 range of current speeds (0.1-1 m/s) in shallow water <1 m.

Sediment traps were fixed (cable-ties and wire) vertically to star-pickets, so the opening sat 0.6 – 0.85 m above the reef surface in kelp beds and on urchin barrens at all four sites. Mean reef depth was 2.32 ± 0.18 , 3.42 ± 0.37 , 3.7 ± 0.58 and 2.62 ± 0.96 m for west, north, southeast and southwest sites respectively. Traps were deployed at three sub-sites locations 50 – 100 m apart within each habitat at each site, and all traps at all sub-sites were recovered, and sediments sampled every 6-8 weeks for 32 months between March 2012 and November 2014.

Particle size distributions (PSD) were measured using a Beckman Coulter LS 13 320 MW laser diffraction particle size analyser (with aqueous liquid module) for wet sediment samples, between April 2012 and February 2014. Two 5 ml replicate subsamples were used to determine PSDs with the mean of both replicates used for statistical analyses. Sediment grain size categories were defined as clay (0.001 – 0.004 mm); silt (0.004 – 0.062 mm); sands (0.062 – 2.00 mm); gravels (2-4 mm). Sediments were oven dried in aluminium trays to constant weight at 100°C, and the dry weight of the sample was used to calculate sediment deposition rate ($\text{g m}^{-2} \text{d}^{-1}$). Sediment deposition of specific grain size fractions were calculated by using the percentage volume in each size fraction described by the PSD and the dry weight of the total sample. Note that due to the shallow nature of the reefs, and often poor weather conditions in PPB, the duration of the sediment deposition time-series varies considerably between sites.

Differences in the mean deposition rate of sediments among habitat (2 factors; kelp bed and sea urchin barren, fixed), site (west, north, southeast and southwest), and season (4 seasons; summer, autumn, winter and spring, fixed) was analysed with an unbalanced

1068 multivariate PERMANOVA of a Euclidean distance matrix of normalised sediment deposition
1069 data.

1070 *Sediment, habitat and site as drivers of recovery potential*

1071 Settlement panels were utilised to enable comparison of algal recruitment on standardised
1072 substrata dependent on sediment treatment, habitat, and site; the panels were employed to
1073 replicate a disturbance that has created free space. At each site (separated by 10s km), 3
1074 replicate experimental stations (separated by 100s m) were established within each reef
1075 habitat (kelp bed and sea urchin barrens, separated by 10s m). Each experimental sub-site
1076 consisted of eight 100 mm x 100 mm black PVC settlement panels, held horizontally at the
1077 same depth by mounting wall brackets to star-pickets. Both upper and lower surfaces of the
1078 panels were sanded to provide roughened settlement surfaces and were held 1 m above the
1079 benthos in order to be well clear of any grazing influence of sea urchins (*H. erythrogramma*;
1080 urchins were not observed to climb the pickets during the experiment) or any effect from
1081 physical disturbance by *E. radiata* thalli.

1082 *Sediment enhancement*

1083

1084 At each sub-site, four panels were randomly allocated to an elevated sediment treatment,
1085 and four were left untreated. Untreated 'control' panels experienced the ambient sediment
1086 load, while the elevated sediment treatment was loaded at double the ambient sediment
1087 load measured at each site see Fig. 2. The treatments were applied every ~42 days; loadings
1088 were specific to each site and habitat (see Table 1). The sediment treatment was composed
1089 of a homogenised mixture of oven dried sediments pooled from sediment traps from all
1090 regions and habitats. A homogenised mixture was used to avoid any potential treatment
1091 effects from altered regional sediment characteristics. PPB is known to have a number of

1092 invasive species which could have been translocated due to the mixing of sediments from all
1093 four regions, however, I mitigate the translocation risk by oven drying the sediments (100°C),
1094 as heat treatment above +80°C has been shown to effectively kill the microscopic stages of
1095 invasive species (Wotton et al. 2004; Tsolaki and Diamadopoulos 2010).

1096 *Assessment of settlement panels*

1097 Every 42 days, prior to addition of sediment, all taxa recruited to the settlement panels were
1098 identified to species level or as functional groups (i.e. canopy former = all Laminariales or
1099 Fucales; understory fleshy algal taxa; ephemeral – taxa known to take advantage of high
1100 resource availability such as *Ulva* spp. and *Cladophora* spp.; turfs; and encrusting coralline
1101 algae (ECA)). Percentage cover of algae was assessed using a 100 x 100 mm grid with 36
1102 intersecting points, and the depth of sediment on the panel was measured to the nearest
1103 mm using a steel ruler.

1104 Temporal trends of taxa on the panels were examined by plotting the univariate time-
1105 series of all functional groups throughout the experiment. Unbalanced nested univariate
1106 PERMANOVAs were used to test the effect of treatment (2 treatments; added and ambient
1107 sediment; fixed), habitat (2 habitats; kelp bed and sea urchin barren; fixed), site (west, north,
1108 southeast and southwest; fixed) and settlement panel sub-site (3 sub-sites nested within
1109 'habitat x site'; random) on the percentage cover of all functional groups at the conclusion of
1110 the experiment.

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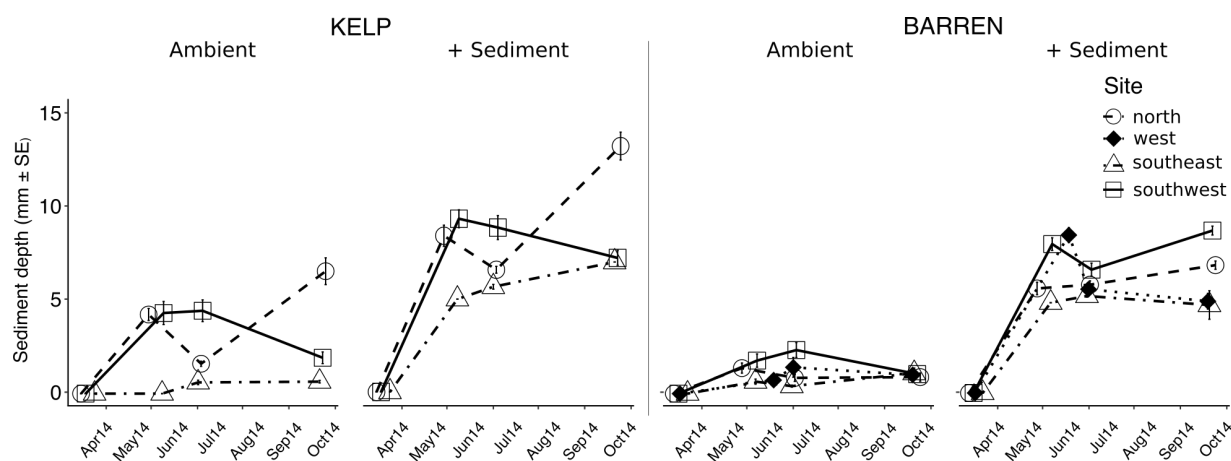


Figure 2. Time-series of sediment depth on 100 x 100 mm settlement panels exposed to treatments of two levels of sediment loading (ambient and 2 x ambient), in two habitats (kelp bed and *Heliocidaris erythrogramma* barren) across the north, west, southeast and southwest sites of Port Phillip Bay.

1121 *Survival and maintenance of Ecklonia radiata*

1122 At each site, three rows of nine star-pickets were set up, two on sea urchin barrens and 1 in
1123 kelp bed habitat. These rows of pickets each formed the central line of a 2 x 10 m swath. In
1124 the urchin barrens, the biomass of the sea urchin *Heliocidaris erythrogramma* in one 2 x 10 m
1125 swath was reduced to half the regional ambient biomass comprising a 'reduced' urchin
1126 treatment (see Table 1). In the second urchin barren area, the urchin density was un-
1127 manipulated as an 'ambient' urchin biomass density treatment (see Table 1).

1128 At each site, a total of 36 kelp individuals were tagged (12 of each Stage I, II and III)
1129 each on individual rocks. From the pool of 36 kelps, 27 (9 of each Stage I, II and III) were
1130 randomly assigned to be transplanted. At the western site, there were no existing beds of *E.*
1131 *radiata*, so kelp was transplanted from the next closest site, i.e. the southwest.
1132 Transplantation involved raising the kelp individuals onto the research vessel and
1133 transporting them between the southwest and western sites taking ~60 minutes. To maintain
1134 the same treatment of all kelp individuals at all sites, I raised all transplanted kelp, at each
1135 site, onto the research vessel and held for 60 minutes in fish bins filled with seawater before
1136 transplanting. The 27 transplanted kelps were randomly assigned to 3 treatments of nine
1137 individuals each (3 of each Stage I, II and III), the 'ambient' and 'reduced' urchin treatment
1138 and the 'handling control' which were transplanted back into the kelp bed, the remaining
1139 nine individuals (not transplanted) stayed in the kelp bed. The rocks of all transplanted kelps
1140 were wired to the star-pickets. All Stage III individuals were hole-punched for productivity
1141 measurements. Every two weeks urchin densities were maintained, and growth, erosion and
1142 survival of individual *E. radiata* was assessed.

1143 Differences in response between the kelp and handling control (i.e. handling control <
1144 kelp) were considered indicative of a negative effect from handling. While differences in
1145 response between reduced and ambient urchins (i.e. reduced > ambient) could be thought of
1146 as impact from elevated urchin biomass density. I ran a logistic analysis on the effect of
1147 treatment (4 treatments; ambient urchin density, reduced urchin density, handling-control
1148 and kelp), site (west, north, southeast and southwest) and life-stage of *E. radiata* (3 life-
1149 stages, 1, 2 and 3 life-stage categories) on survival of *E. radiata* following two months of
1150 experimental treatment. Differences in survival were assessed using a binomial regression.
1151 Gross production rate (g(dw) d^{-1}) was analysed among treatment (4 treatments; ambient
1152 urchin density, reduced urchin density, handling-control and kelp) and site (west, north,
1153 southeast and southwest) as fixed factors using balanced univariate PERMANOVA.

1154

1155 *Statistical analyses*

1156

1157 *Univariate PERMANOVA*

1158 Univariate PERMANOVAs (using PRIMER-E V7 with PERMANOVA add-on Clarke and Gorley

1159 2015) were used because PERMANOVA makes no assumptions about the distribution of

1160 errors. Variables for univariate PERMANOVAs were log-transformed and PERMANOVAs were

1161 computed on Euclidean distance matrices using 9999 permutations and unrestricted

1162 permutations of raw data to generate P-values. Type III sums of squares were utilised to

1163 accommodate the unbalanced nature of some designs. Permutational post-hoc t-tests were

1164 used to test pair-wise combinations of groups for significant effects (Clarke et al. 2014).

1165 Global and pair-wise PERMDISP was also used to understand the nature of the significant

1166 differences, i.e. whether significance was driven by differences in the mean, the dispersion of

1167 the variable, or both. In cases with insufficient permutation, P-values were obtained by

1168 Monte-Carlo tests (Clarke et al. 2014).

1169 *Canonical analysis of principal coordinates*

1170 Canonical analysis of principal coordinates (CAP) was used to visualise the highest order

1171 significant sources of variability, on which I overlaid vectors from Spearman correlations

1172 ($R > 0.5$) and bubble plots to visualise key drivers of the observed separation (Clarke et al.

1173 2014).

1174 *Binomial regression*

1175 Differences in binomial variables were assessed using a binomial regression via 'glm' in base

1176 R, R package version 3.1.2 (R Development Core Team 2015) with sequential model selection

1177 and table building using the 'AICcmodavg' package (Mazerolle 2011). I used 'predict' in the

1178 MASS package (Venables and Ripley 2002) to estimate the probability of survival due to

significant factors. I undertook pair-wise Tukey's tests using 'glht' in the multcomp package (Hothorn et al. 2007) to assess significance within factors. All R analysis was undertaken via R version 3.1.2 (R Development Core Team 2015) running in RStudio version 1.0.136 (RStudio Team 2015)

1183

1184 Results

1185

1186 *Reproductive output*

1187

1188 Zoospore release assays for *Ecklonia radiata* show a clear reproductive season between
1189 January and May with total zoospores per *E. radiata* thallus peaking at $1.8 \times 10^6 \pm 1.6 \times 10^6$,
1190 $1.8 \times 10^7 \pm 2.8 \times 10^6$ and $3.4 \times 10^7 \pm 4.7 \times 10^6$ (mean \pm SE) for the southeast, southwest and
1191 north respectively. While there is a definite seasonal peak in zoospore release, *E. radiata*
1192 produces zoospores throughout the year (Fig. 3a).

1193

1194 *Patterns of zoospore supply and recruitment of Ecklonia radiata*

1195

1196 Interestingly, high densities of Stage III (Table 2) thalli in the southwest ensured a propagule
1197 pressure equivalent to that at the northern site, despite lower overall zoospore release per
1198 sporophyte in the southwest (Fig. 3a and c). Conversely, due to the low density of
1199 reproductive *E. radiata* in the southeast, propagule pressure at this site was low (Fig. 3c).
1200 High propagule pressure translated to high numbers of recruiting Stage I thalli in the
1201 southwest (Fig. 3e), but not in the north where the recruitment rate was similar to that in the
1202 southeast. Stage I *E. radiata* thalli are present throughout the year but peak in density in
1203 spring (September – November), with peak propagule pressure occurring over the period of
1204 lowest densities of stage I *E. radiata* (Fig. 3c and e).

Variability in sediment deposition due to site and habitat

Sediment deposition was similar on kelp beds and sea urchin barrens through most of the sampling period, however during periods of highest sediment deposition (i.e. spring and summer), rates in kelp beds in the north and southeast were greater than double that experienced in adjacent sea urchin barrens (Table 1; Fig 4a, b and c). The multivariate analysis of deposition rates showed significant differences in deposition rates by size fraction. However, this relationship was complex as reflected by a significant 'habitat by region by season' interaction (Table 3). The total deposition was similarly high in kelp habitats in the north and the southeast, however a greater proportion of sediment deposition in the north and west was comprised of fines >63 μm , whereas in the southeast, there was a greater proportion of gravels and sands (Fig 5a and b).

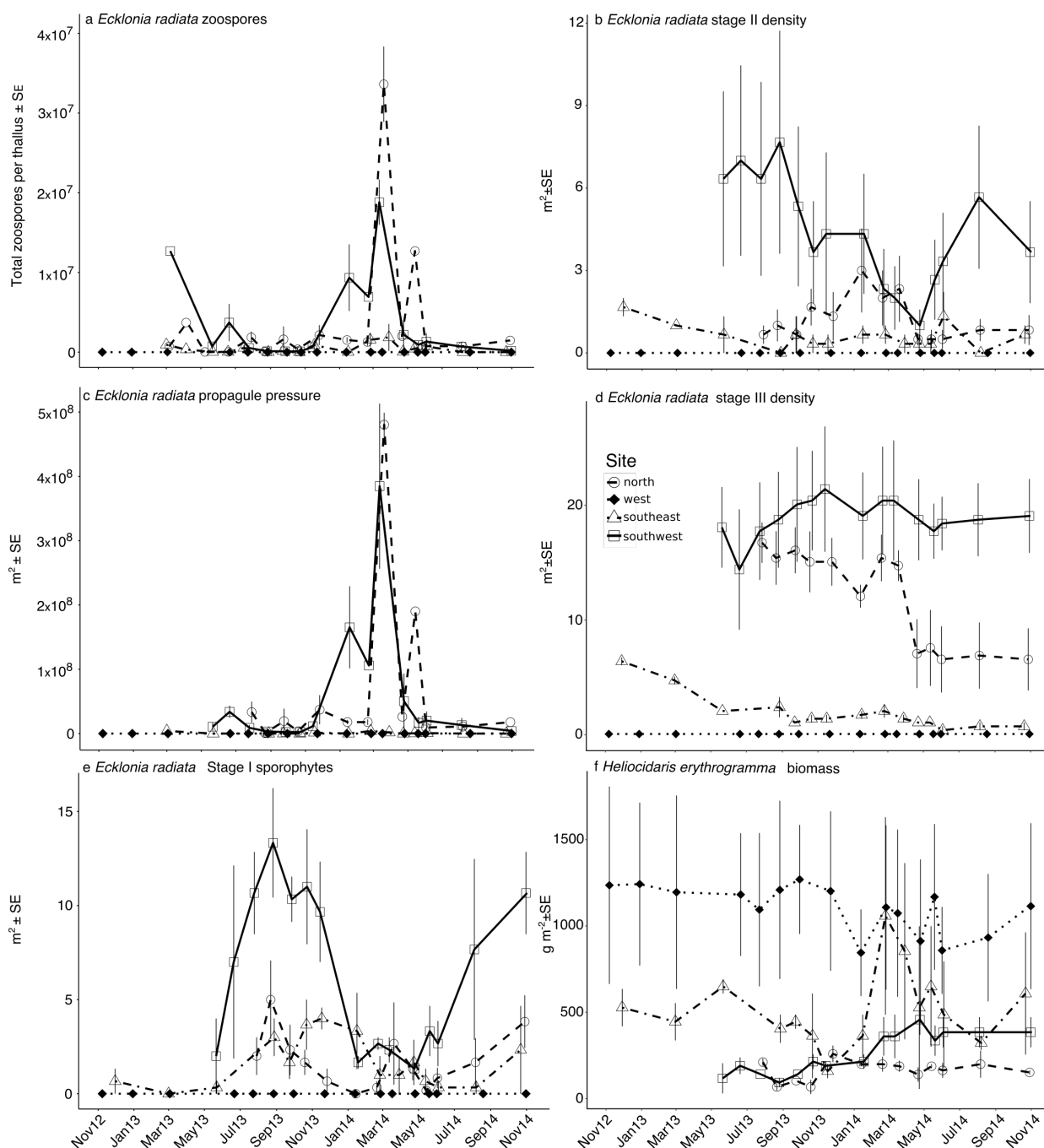
1227 Table 2. Estimated propagule production and proportional survival between life-stages of *Ecklonia radiata* in Port Phillip Bay.

1228

Site	Annual propagule production (sp indiv ⁻¹ yr ⁻¹)	Annual propagule pressure (sp m ² yr ⁻¹)	Max Stage I (m ²)	Proportional survival - spore to Stage I	Max Stage II (m ²)	Proportional survival - Stage I to Stage II	Stage III (m ²)
west	0	0	0	0	0	0	0
north	1.60x 10 ⁹	2.28x 10 ¹⁰	9	1.27x 10 ⁹	6	0.67	9-20
southeast	1.90x 10 ⁸	3.00x 10 ⁸	7	2.14x 10 ⁷	3	0.43	0-7
southwest	1.56x 10 ⁹	3.04x 10 ¹⁰	18	8.43x 10 ⁸	15	0.83	6-32

1229

1230



1231

1232 Figure 3. Time-series plots of *Ecklonia radiata* (a) zoospores produced per sporophyte ($n=6$); (b) *E.*
 1233 *radiata* Stage II sporophytes; (c) propagule pressure; (d) *E. radiata* Stage III sporophytes; (e) *E. radiata*
 1234 stage I (recruit) density, and (f) *Heliocidaris erythrogramma* biomass density for four sites in Port
 1235 Phillip Bay through 25 months from November 2012 to 2014. Data are means ($n=3$) \pm SE.

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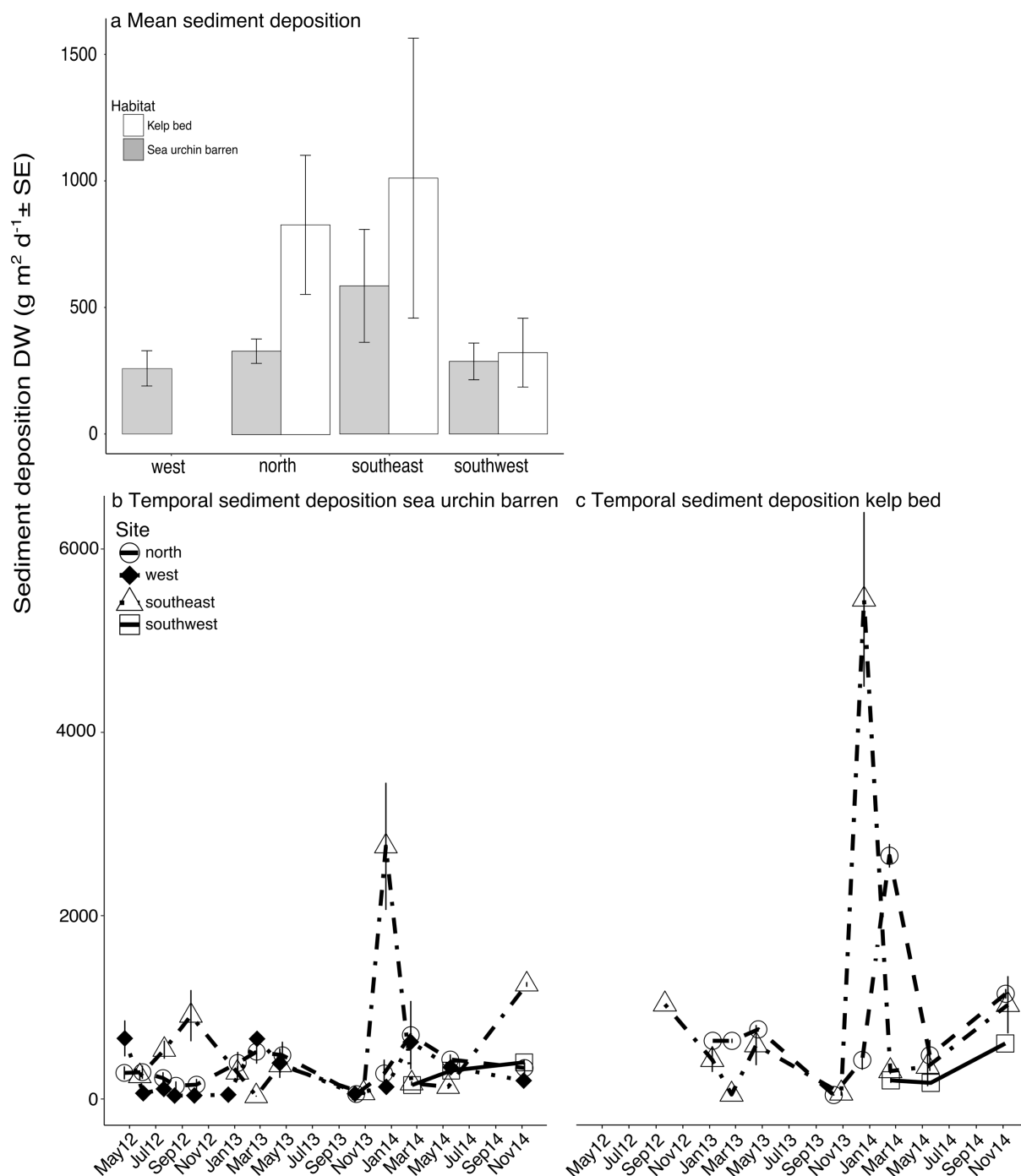


Figure 4. a) Mean sediment deposition rates for a period of 31 months between May 2012 and November 2014 (mean $\text{g m}^{-2} \text{d}^{-1} \pm \text{SE}$) in *Heliocidaris erythrogramma* urchin barren and kelp bed habitat at four sites across Port Phillip Bay (north, west, southeast and southwest); b) Time-series of mean sediment deposition ($n=3$, mean $\text{g m}^{-2} \text{d}^{-1} \pm \text{SE}$) in sea urchin barrens and c) kelp beds for the 4 regions: west – diamond and dotted line; north – circle and dashed line; southeast – triangle and dot-dash line and southwest – square and solid line.

Table 3. Results of a 3-way PERMANOVA testing the significance of effects of Habitat (2 levels: kelp bed and sea urchin barren), Site (west, north, southeast and southwest), and Season (4 levels: spring, summer, autumn and winter) on normalised size-fractions of deposited sediment. df = degrees of freedom, Pseudo-F test values are computed from 9999 permutations. ● $p > 0.05 < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, † indicates one or more empty cells in the term

Source	df	Pseudo-F
Habitat (fixed)	1	1.28
Site (fixed)	3	8.19***
Season (fixed)	3	8.50***
HabitatxRegion†	2	1.79
HabitatxSeason	3	1.66
RegionxSeason†	6	6.17***
HabitatxRegionxSeason†	3	2.48*
Error	41	

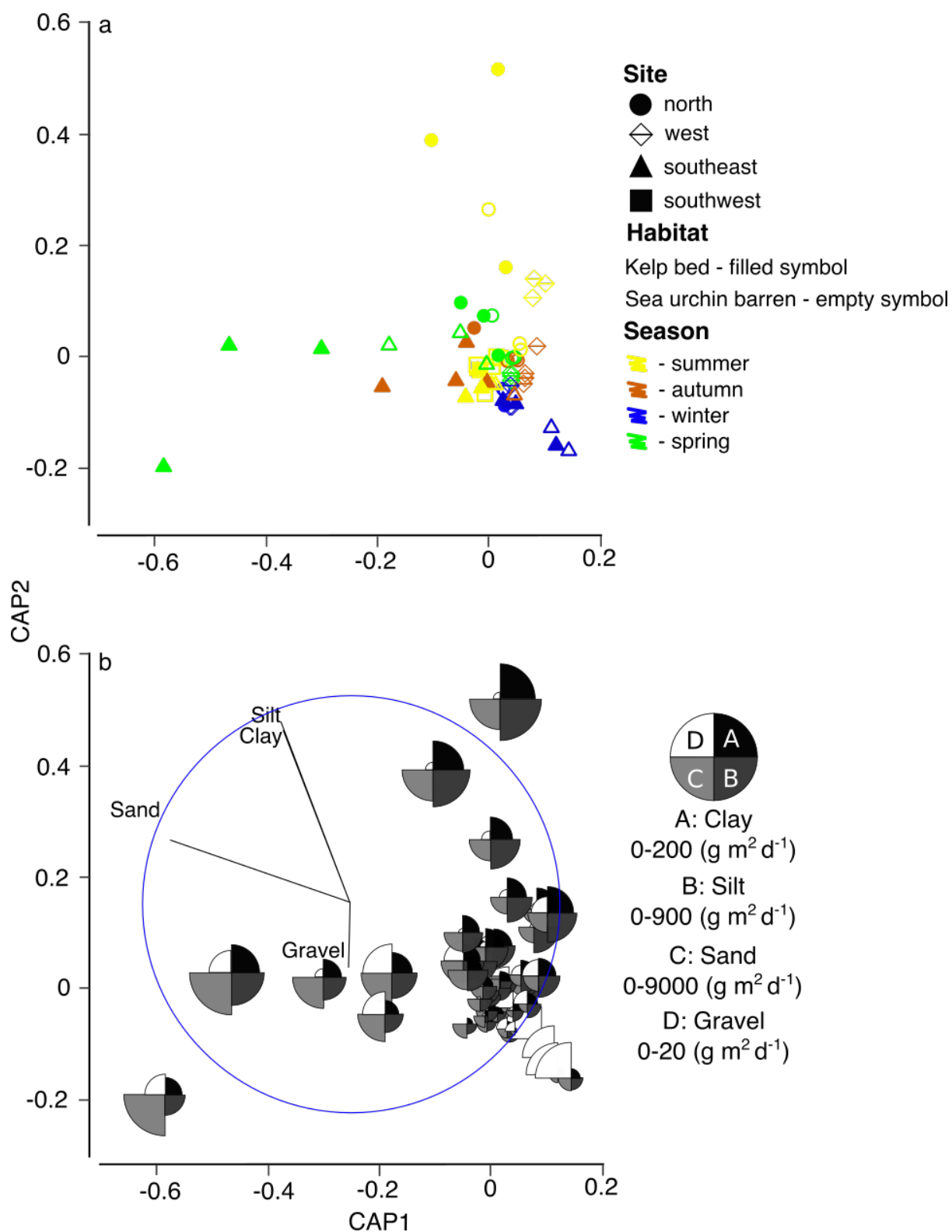


Figure 5. Canonical analysis of principal coordinates plots exploring a Site x Habitat x Season model of sediment deposition characteristics (mean, $n=3$) a) CAP displaying the pattern of sediment deposition b) displays a bubble CAP for sediment deposition decomposed into size-fractions of Clays (0.001 - 0.004 mm) – black quadrant in position A; Silts (>0.004 - 0.062 mm) – dark grey quadrant in position B; Sands (>0.062 - 2.00 mm) – light grey quadrant in position C and Gravels (>2-4 mm – white quadrant in position D with a vector (Pearson correlation >0.05) plot showing the size-fraction of sediment that is driving the separation in (a) and (b).

Variability in kelp bed recovery potential due to site and habitat

'Site' was the main factor determining variability in patterns of algal recruitment on settlement panels, with 'Site' either as a significant main effect or interacting with 'Treatment' or 'Habitat' (Fig. 4 and Table 4). Additionally, significance of the nested 'Station' term indicated considerable variability in algal recruitment at fine spatial scales (i.e. between reef areas in the same habitat and region 100 m apart) (Table 4). PERMDISP and pair-wise PERMDISP, as companion tests to PERMANOVAs, identified that the majority of significant tests were derived from both dispersion effects (differences in the spread of the group data clouds) and location effects (difference in the mean of groups) (Table 4). A generalisable pattern was that panels in kelp beds always became dominated by a single functional group differentiated by site at the conclusion of the experiment (i.e. canopy-formers in the southeast, turfs in the north and understory reds in the southwest). Whilst for sea urchin barrens a greater number of species co-existed on the panels (Fig. 6).

Free-space and canopy formers

At all sites, there was a rapid decline in available space on the settlement panels as a result of recruitment of algae. The rate of space utilisation was greater and less variable in kelp beds than in sea urchin barrens (Fig. 6f). Recruitment of canopy-formers took ~5-6 months to occur (Fig. 6a), but with little to no cover of canopy-formers observable in any region or habitat other than on the panels in southeast kelp beds ($48.8 \pm 38.4\%$, mean \pm SE). At all other sites other taxa appeared to be better competitors for space on the panels than canopy-formers.

1294 *Turf*

1295

1296 Within kelp beds, turf was quicker to monopolise free-space than on settlement panels on
 1297 sea urchin barrens (Fig. 6d). Turf cover in kelp maintained coverage at ~100% in the north,
 1298 and peaked at $91.9 \pm 22.1\%$ (mean \pm SE) in the southwest and $62.0 \pm 35.5\%$ in the southeast
 1299 two months after the experiment commenced (Fig. 6d), but had reduced to ~0% cover on
 1300 panels in the southeast and southwest by the final sampling period. On sea urchin barrens in
 1301 the north, turf cover reached $54.4 \pm 8.1\%$ after two months, and retained consistent high
 1302 cover for the remainder of the experiment (Fig. 6d). Turf on settlement panels on urchin
 1303 barrens at other sites (particularly in the southwest) took longer to develop than in the north,
 1304 reaching maximal coverage six months into the experiment following loss in cover of other
 1305 dominating taxa, but had reduced to lower coverage by the conclusion of the experiment
 1306 (23.9 ± 7.9 , 19.1 ± 0.9 and $5.3 \pm 4.4\%$ (mean \pm SE), as southwest, southeast, and west
 1307 respectively).

1308

1309 *Ephemeral taxa*

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1311 Ephemerals, while not a dominant guild, achieved higher cover on settlement tiles in sea
 1312 urchin barrens in the west and north than in other habitats and regions (Fig. 6c). Similar to
 1313 turfs, patterns in the final cover of ephemerals was driven by the interaction of region and
 1314 habitat (Table 4).

1315

1316 *Understorey*

1317

1318 The time-series plots (Fig 6b) show distinctly different patterns in cover of understorey algae
 1319 between habitats. Kelp habitats produced a low cover of understory taxa, apart from in the
 1320 southwest where understory cover increased markedly in the last two months of the

1321 experimental period (Fig. 6b). On sea urchin barrens, understory cover increased rapidly to
1322 ~100% in the southwest within the first two months then declined (Fig. 6b). In the west and
1323 north, cover of understory algae gradually proliferated throughout the experiment.

1324

1325 *Encrusting coralline algae*

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1327 The pattern of colonisation of plates by encrusting coralline algae (ECA) was similar to that
1328 for canopy-formers, as the southeast was the only site where ECA was observed above 0.5%
1329 cover. ECA was the only variable in which the PERMANOVA analysis detailed any effect of
1330 elevated sedimentation; under elevated sedimentation in the southeast ECA increased to
1331 almost double the cover of ECA under ambient sedimentation (57.1 ± 32.5 compared to 27.7
1332 $\pm 35.8\%$) (Fig. 6e).

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1345 Table 4. Results of a 4-way unbalanced PERMANOVA testing the significance of sediment loading (2
 1346 levels: ambient and elevated sedimentation – fixed), Habitat (2 levels: kelp bed and sea urchin barren
 1347 – fixed), Site (west, north, southeast and southwest – fixed) and Sub-site(settlement panels stations
 1348 x3, nested in Habitat x Site – random). Data are log transformed percentage cover for Free-Space;
 1349 ECA = encrusting coralline algae; Turf = turf-sediment matrix; Ephemeral = ephemeral algae taxa such
 1350 as *Ulva* spp. moreover, *Cladophora* spp.; Understory = all fleshy taxa beneath the canopy excluding
 1351 ephemerals and turfs; Canopy = canopy-forming algae from Laminariales and Fucales; Hill number N1
 1352 or effective number of species = measure of diversity. df = degrees of freedom; Pseudo-F estimates
 1353 are computed from 9999 permutations. Additionally, PERMDISP tests are shown for the highest order
 1354 interactions for each test for pair-wise t-values see Appendix 4.

		Free-Space						
			ECA	Turf	Ephemeral	Understory	Canopy	Richness
		Pseudo						
Factors	df	Pseudo-F	Pseudo-F	Pseudo-F	Pseudo-F	Pseudo-F	-F	Pseudo-F
Treatment (T)	1	1.17	8.95*	0.29	0.19	0.24	0.93	0.009
							59.49*	
Habitat (H)	1	0.19	2.01	0.01	2.43	2.15	*	0.41
							43.49*	
Site (S)	3	1.56	26.38**	17.03**	4.98*	7.69***	*	0.85
T*H	1	0.49	2.42	0.57	0.13	0.1	1.45	1.03
T*S	3	0.49	9.19**	1.91	0.81	0.67	0.32	1.04
							65.82*	
H*S?	2	0.38	1.3	4.57*	2.89	3.35	**	1.97
Station(H*S)	13	2.27*	6.06**	1.9*	1.21	0.89	2.43*	6.33*
T*H*S?	2	0.31	1.16	0.59	1.91	0.79	1.74	0.13
T*Station(H*S)?	12	1.46	2.14*	0.98	0.44	0.79	2.27	0.92
Error	91							
PERMDISP								
	3,1							
Site (S)	26	-	-	-	75.14***	-	-	-
	7,1							
T*S	22	-	44.49***	-	-	-	-	-
	6,1						26.83*	
H*S?	23	-	-	20.72***	-	5.94***	*	-

● $p > 0.05 < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, ? indicates one or more empty cells in the term

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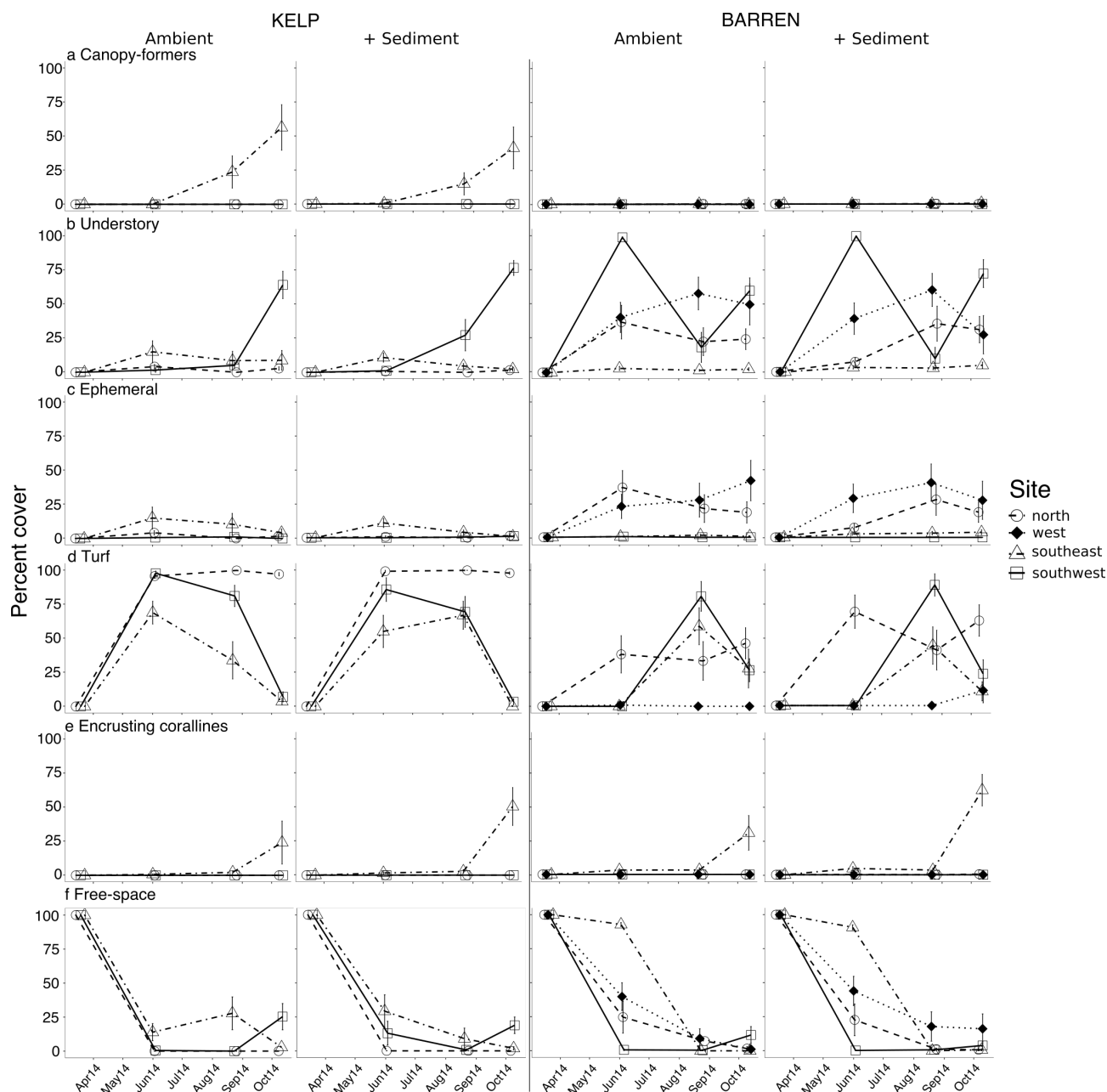


Figure 6. Time-series trajectories of percentage cover of functional groups of algae on 100 x 100mm settlement panels exposed to treatments of 2 levels of sediment load (ambient and 1 x ambient), in 2 habitats (kelp bed and *Heliocidaris erythrogramma* barren) in the four sites of Port Phillip Bay. Functional groups are (a) canopy-forming algal taxa (Laminariales and Fucales); (b) understory algal taxa (all fleshy taxa beneath the canopy); (c) ephemeral algal taxa (largely *Ulva* spp. and *Cladophora* spp.) know to benefit from high resource availability excluding the turf-sediment matrix); (d) turf-sediment matrix; (e) encrusting coralline algae; and (f) free-space over 7 months between April and October 2014. Data are means ($n=12$) \pm SE.

Patterns in regional sea urchin biomass and kelp post-settlement dynamics

Heliocidaris erythrogramma biomass

The western site had the highest and most variable urchin biomass per unit area, but mean biomass remained relatively stable throughout the two-year sampling period. The southeast showed highly changeable mean urchin biomass with a peak in March 2014 of 3x the minimum biomass. Urchin biomass in the north and southwest approximately doubled over the sampling period (Fig. 3f).

Ecklonia radiata Stage II thalli

Timing in the peak in density of Stage II thalli varied between regions. In the southwest, the peak occurred in spring (September) at a similar time to the peak in Stage I settlement. In the north, density of Stage II algae peaked in mid-summer (January), while for the southeast there was no clearly defined peak in density (Fig 3b).

Ecklonia radiata Stage III thalli

The density of stage III thalli was greatest in the southwest, with densities of reproductive thalli remaining stable throughout the sampling period. In the north, the density of Stage IIIs was similar to that in the southwest at the beginning of the sampling period, but there was a significant decline in autumn 2014 (March-May). The southeast showed a continual decline throughout the sampling period (Fig. 3d).

Ecklonia radiata growth and loss

The highest growth rates of sporophytes occurred in spring and summer 2013, while the lowest rates occurred in late autumn and winter (Fig. 7a). The north and southwest showed peak rates of loss in spring and summer, while in the southeast highest losses of sporophyte biomass were in autumn and winter (Fig. 7b). Figure 7c shows that *E. radiata* are generally losing biomass through the majority of the growing season in PPB, with net positive addition to thalli biomass only occurring in spring (September – November).

Sea urchins as drivers of survival and maintenance of Ecklonia radiata

Survival of Ecklonia radiata thalli

The best-fit model was the 3-term additive model (see Appendix 4 for model fitting), all three main terms were strongly significant (Table 5a). No difference in survival was detected between unmanipulated *E. radiata* left in the kelp bed and those treated as handling controls (Table 5b), so evidence of reduced survival was attributable to the treatment as opposed to the transplant procedure. Multiple-comparison tests show that survival of *E. radiata* thalli was greatly reduced in the southeast, with estimates suggesting only 15 out of 100 *E. radiata* would survive a two-month period. Survival of *E. radiata* on reefs at all other sites was broadly similar ranging between 70 – 84% (Table 5b). The presence of ambient urchin biomass at all regions resulted in reduced survival of sporophytes. relative to experimental reductions of urchins, regardless of the life-stage of *E. radiata* (Table 5b). Reducing urchin biomass on barrens by half increased survival of *E. radiata* thalli from ~25 to 77%, which is similar to the survival rates observed in kelp beds. Survival of *E. radiata* was also dependent on sporophyte life-stage, with Stage I sporelings 20% less likely to survive than the larger more developed Stage II and III thalli (Table 5b).

1424 *Growth of Ecklonia radiata thalli*

1425

1426 There was no evidence that net growth of surviving kelps differed among urchin treatments

1427 and there was no evidence of differences in net growth among sites, most likely due to high

1428 variability in the net change in Stage III thallus size. All net blade growth was negative or with

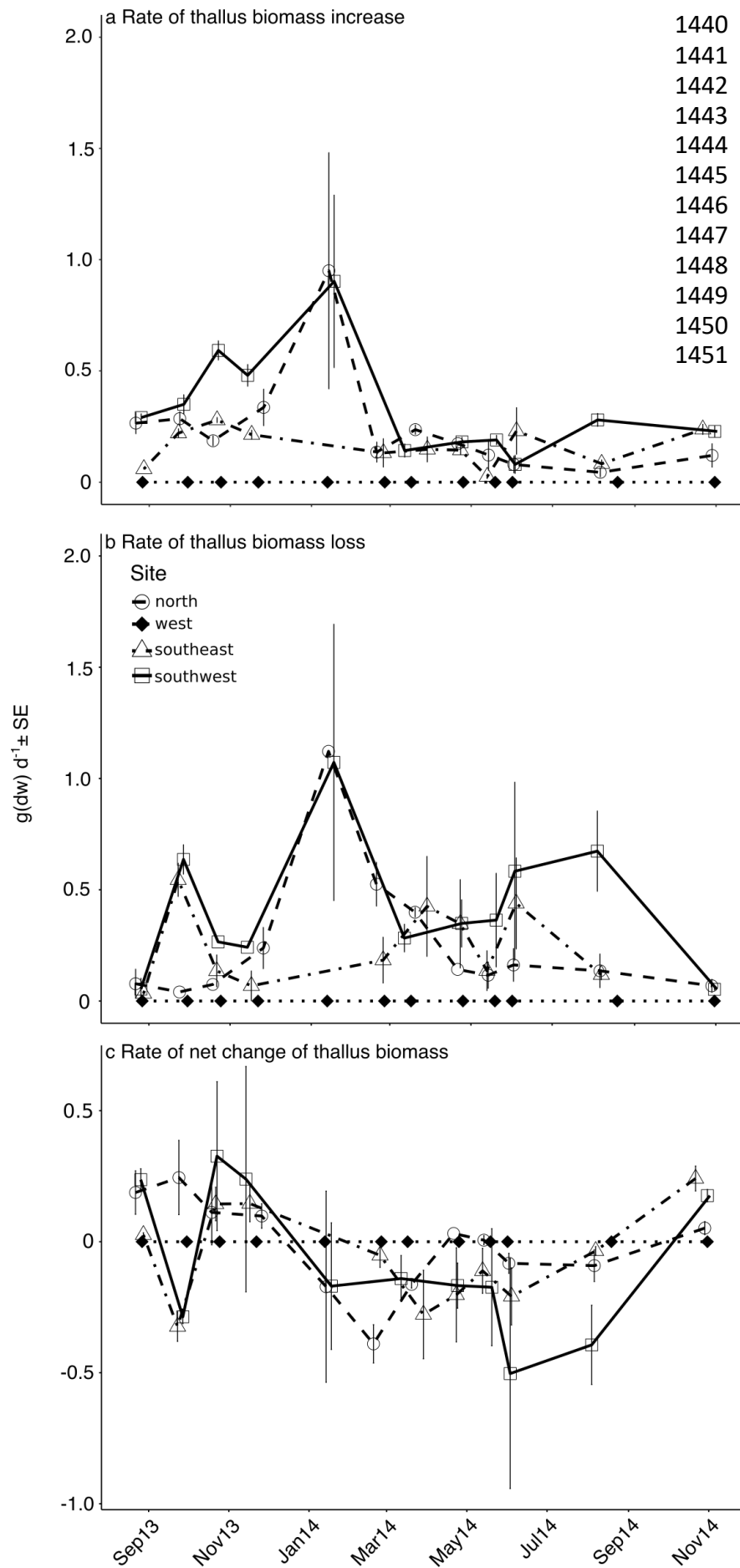
1429 error bars overlapping zero, apart from in the west (Fig. 8).

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Table 5. Logistic regression results showing the effects of: (a) Site (4 levels: west, worth, southeast and southwest), Treatment (4 levels kelp bed, procedural control, ambient and reduced sea urchin biomass on barren habitat), and life-stage (3 levels: Stage I, Stage II and Stage III) on the survival of *Ecklonia radiata*; (b) Region (3 levels: north, southeast and southwest), Taxa (2 levels: Laminariales and Fucales), and life-stage (2 levels: juvenile i.e. non-reproductive individuals and adults reproductive sporophytes) on the likelihood of finding sporophytes attached to stable versus unstable substrata. Hierarchies of significance from Tukey's tests and estimates of survival probabilities (a) and attachment probabilities (b) are shown.

a.					
Source	df	Deviance	Resid.Df	Resid.Dev	P-Value
Site	3	28.046	35	74.711	3.55e-06***
Treatment	3	41.229	32	33.482	5.85e-08***
Life-stage	2	8.899	30	24.584	0.01169
Parameter	Tukey's test				
Region	N&SW&W>>SE				
Treatment	Kelp&Control&Reduced>Ambient				
Life-stage	Stage 3 > Stage 2 & Stage 1				
Estimated survival probability				SE	
Site: W		0.76		0.08	
Site: N		0.7		0.1	
Site: SE		0.25		0.11	
Site: SW		0.84		0.07	
Treatment:Kelp		0.82		0.07	
Treatment:Control		0.77		0.08	
Treatment:Reduced		0.72		0.1	
Treatment:Ambient		0.25		0.12	
Life-stage:1		0.52		0.1	
Life-stage:2		0.68		0.09	
Life-stage:3		0.72		0.08	
b.					
Source	df	Deviance	Resid.Df	Resid.Dev	P-Value
Site	2	66.8	9	78.48	3.13e-15***
Taxa	1	47.51	8	30.97	5.48e-12***
Life-stage	1	20.86	7	10.11	4.94e-06***
Parameter	Tukey's test				
Site	SE=N, SE>SW				
Taxa	Furoid>>Kelp				
Life-stage	Adult>>Juvenile				
Estimated probability of attachment to stable substrate				SE	
Site:N		0.85		0.05	
Site:SE		0.94		0.02	
Site:SW		0.79		0.05	
Taxa:Laminariales		0.77		0.05	
Taxa:Fucales		0.96		0.03	
Life-stage:Juvenile		0.77		0.06	
Life-stage:Adult		0.96		0.02	

●p>0.05<0.1, *p<0.05, **p<0.01, ***p<0.001



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Figure 7. Time-series plots of rates of (a) thallus biomass increase, (b) thallus biomass loss, and (c) net change in thallus biomass for the four sites in Port Phillip Bay through 15 months from September 2013 to November 2014, data are means ($n=3$) \pm SE.

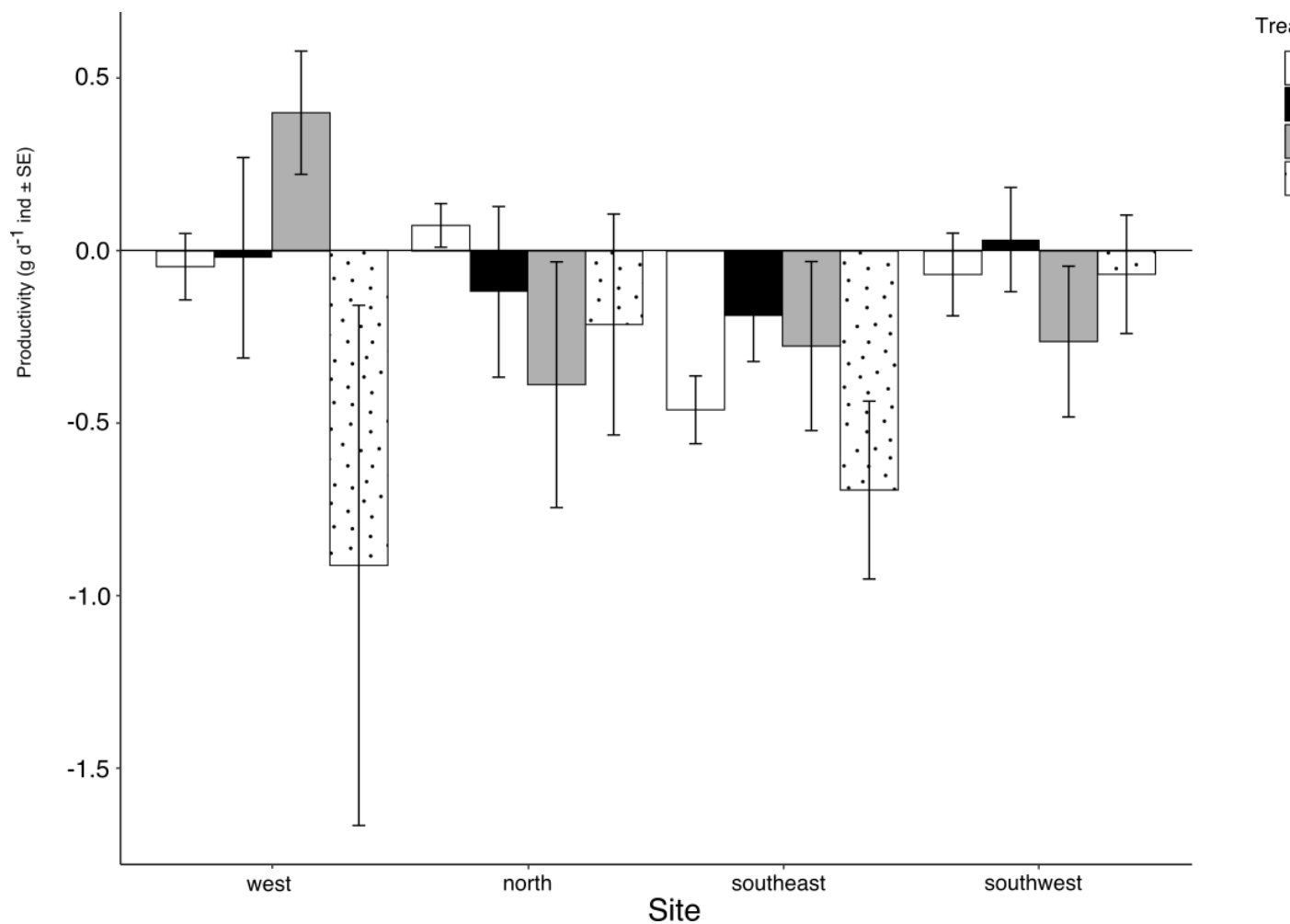


Figure 8. Rate of net change in thallus biomass of *Ecklonia radiata* Stage III sporophytes in 4 sites across Port Phillip Bay exposed to 4 treatments (Control 1 – white: procedural control where kelps were exposed to the same transplant process but put back into the kelp bed; Control 2 – black: kelp plants were unmanipulated and left in place in the kelp bed; Reduced – grey: kelp thalli were transplanted from the kelp bed to *Heliocidaris erythrogramma* barrens but with urchin biomass reduced to half of ambient; and Ambient – dotted: kelp plants transplanted to *H. erythrogramma* barrens with ambient urchin biomass) for 2 months from April and May 2014. Data are means ($n=3$) \pm SE.

Discussion

Our observations of kelp population dynamics across three key life-history phases (i.e. pre-settlement, settlement and post-settlement) at multiple sites and habitats indicate that recovery potential and resilience of kelp beds in Port Phillip Bay are limited primarily by extrinsic factors such as the identity of local species pools and sea urchin grazing. The bottlenecks that occur at each life-history stage are thus the result of reduced survival via grazing and competitive processes that act to drastically reduce the number of 'safe sites' for kelp recruitment.

Pre-settlement

Kelps, in general, are extremely fecund, producing up to 10^8 – 10^{12} spores sporophyte⁻¹ year⁻¹ (Schiel and Foster 2006). Reproductive output of *Ecklonia radiata* was similar in PPB to the reproductive output recorded for other kelps (Kain and Jones 1975; Chapman 1984; McConnico and Foster 2005; Schiel and Foster 2006; Mohring et al. 2013). The timing of seasonal maxima in propagule supply and the synchrony in timing of reproduction of *E. radiata* in PPB is similar to that observed by Mohring et al. (2013) in Western Australia, where peak zoospore supply occurred from midsummer through to the end of autumn. Synchrony of reproduction in kelps is likely to increase fertilisation success of gametophytes, and increase the likelihood of recolonisation following disturbance (Reed et al. 1997; Mohring et al. 2013). There was little evidence of any alteration to natural cycles of spore production in PPB. However, not all sites were equal regarding the number of spores produced.

Spore production per unit of reef in PPB varied significantly among sites and was determined primarily by the density of sporophytes, although there were also differences in the number of spores produced per individual among sites, reflecting phenotypic variability in *E. radiata*. *E. radiata* at the southeastern site were small, with a smaller absolute area of sorus tissue, and produced fewer spores per unit area of sorus. Fecundity and the timing of reproduction have been linked to thallus biomass in other kelp (Mohring et al. 2013). Reed (1987) observed that *Macrocystis pyrifera* during periods of high nutrient concentrations were able to grow large and apportion more energy for gamete production. Phenotypic plasticity in *E. radiata* and other kelps suggest that differences in abiotic variables such as nutrient concentrations, exposure and temperature can drive changes in phenotype influencing both survival and reproduction (Serrao et al. 1996; Kawamata 2001; Wernberg et al. 2003; Mohring et al. 2013; Flukes et al. 2015). The timing of reproduction in most kelps is often synchronised to periods of favourable environmental conditions, such that propagules are released during favourable conditions ensuring the greatest chance of successful dispersal, settlement, growth and survival (Reed 1987; Reed et al. 1997; Mohring et al. 2013).

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1500 ***Settlement***

Estimates of proportional survival from spores to Stage I sporophytes (visible recruits) for *E. radiata* in PPB were 2 to 4 orders of magnitude smaller than estimates reported for other similar intertidal and subtidal kelp species (e.g. *Alaria marginata* McConnico and Foster, 2005; *Laminaria longicruris* and *L. digitata*, Chapman 1984). There were also distinct differences in proportional survival among regions. On the southern reefs, there were contrasting amounts of propagule supply (i.e. southwest = high; southeast = low). However, proportional survival at the two sites was similar. In contrast, propagule supply in the north

1508 was high and similar to the southwest, but proportional survival in the north was much lower.
1509 The absence of sporophytes in the west suggests that at this site *E. radiata* is locally extinct.
1510 Large scale physical oceanographic processes, such as boundary currents, are known to
1511 influence connectivity of kelp populations (Coleman et al. 2011a and b), with weaker
1512 connectivity occurring with slower moving currents. Durrant et al. (2014) suggest that a
1513 distance of < 50 km is sufficient to limit the effects of isolation by distance on connectivity for
1514 a range of macroalgae (intertidal and subtidal Rhodophyta, Phaeophyta, Chlorophyta). As
1515 such the distances between reefs seems to be sufficient to ensure connectivity among reefs
1516 in PPB, assuming sufficient and consistent coastal currents. Thus, the lack of kelps in the west
1517 could be the result of complex nearshore circulation patterns that limit connectivity of kelps
1518 among reefs in PPB (Coleman et al. 2011a and b). Additionally, low survival in the period
1519 between spore and macroscopic sporophyte could arise for a multitude of other reasons,
1520 including poor spore survival in the water column, low spore settlement, poor gametophyte
1521 development, survival, or maturation, reduced fertilization success, or high mortality of
1522 microscopic sporophytes (Schiel and Foster 1986; Schiel and Foster 2006). Our study did not
1523 investigate these mechanisms, highlighting the need for further work to understand
1524 connectivity among populations and factors limiting survival from gamete to sporophytes in
1525 kelps. Nevertheless, the settlement panel experiment did highlight that the identity of early
1526 colonisers was important in the provision of available substrate to support 'safe' and
1527 successful development of kelp early life stages.

1528

1529 'Safe sites' (sensu Harper, 1965) define suitable patches that support the safe
1530 development of a species' propagules (Green 1983). Safe sites for the recruitment of kelp are
1531 spatially and temporally highly variable, and are likely strongly related to density-dependent

effects from adult conspecifics; as adult kelps can have both positive and negative effects on settlement and early-stage survival of juvenile seaweeds through various mechanisms. The settlement panel experiment aimed to both limit the effects of grazing, and also the direct negative effects of adult kelps on recruitment (i.e. shading and scour from the lamina) by holding the panels off the substrata and above the kelp canopy. In doing this I also reduced any positive effect the adult kelps might have on recruits, such as reducing accumulated sediment (Irving and Connell 2002b; Gorman and Connell 2009) or interspecific competition (Toohey et al. 2007; Wernberg 2009).

Perhaps the most striking result from the settlement panels experiment was the lack of kelp recruitment and overwhelming dominance of turf on the panels in the kelp beds of the north, which was in stark contrast to the recovery of canopy-formers on panels in the kelp beds of the southeast. The response of the communities that developed in the north is evidence of founder control, in that taxa that initially colonised the panels remained dominant throughout the experiment. In contrast, after two months panels in the southern kelp beds, showed reduced dominance of turf, due to displacement by canopy-forming fucoids and ECA in the southeast. The strong founder effect in the north contributed to a reduction in available safe sites for recruitment of kelps, while limited founder control, extensive free-space and good colonisation of ECA in the southeast provided an abundance of safe sites resulting in high recruitment of canopy-forming fucoids.

It is also apparent that the identity of the canopy-formers plays a role in recovery potential. The kelp bed in the north was dominated solely by *Ecklonia radiata* while in the southeast the kelp bed comprises some *E. radiata*, but also many fucoid algae. It was therefore interesting that the sole contributor to kelp recovery on the panels in PPB was not

E. radiata, but *Caulocystis* spp., a furoid. The life-history of fucoids lacks a free-living gametophyte stage, unlike that of laminarians, typically resulting in furoid survival several orders of magnitude greater than that experienced by the microscopic stages of laminarians (Schiel and Foster 2006). Therefore, I suggest that intrinsic factors such as differences in biology, i.e. no free-living gametophyte (Schiel and Foster 2006), the ability to float on detachment (Bennett and Wernberg 2014), and reduced vulnerability to sea urchin grazing from high secondary metabolic content (Steinberg 1989) of fucoids contributes to higher dispersive capacity and recovery potential of furoid canopy-formers in the southeast relative to *E. radiata*. It is also apparent that *E. radiata* recruitment is more dependent on facilitation by adult canopy than fucoids (Bennett and Wernberg 2014). Concerningly, this suggests that *E. radiata* have a poor competitive capacity, particularly in early life-history. Our results are similar to findings elsewhere that also show dominance by turfs following loss of canopy-forming macroalgae along many urbanised coastlines (Eriksson 2002; Airoidi 2003; Connell et al. 2008).

The collective evidence from other studies suggests that positive feedbacks maintain kelps when kelp is dominant and alternatively turf when turf is dominant. When kelps are present they reduce light to the substratum (Reed and Foster 1984; Connell 2005; Wernberg et al. 2005), and while their effect in reducing water motion increases sedimentation (Eckman et al. 1989), the direct physical action of kelp thalli removes sedimentation and the turf algae that binds and traps sediment. Reduction of water motion by kelps can also help retain spores and pheromones necessary for release of sperm from male gametophytes (Lüning and Müller 1978). Additionally, kelp can metabolically modify seawater pH via photosynthesis and respiration, and these diurnal pH fluctuations can enhance kelp growth,

particularly of juvenile stages (Britton et al. 2016). Conversely, when kelps are removed and turfs establish, turf morphology acts to trap and retain sediment, which accumulates to form a consolidated turf-sediment matrix, which is widely known to reduce or completely prevent kelp recruitment. The exact mechanism is unclear but has been linked to competition for space, chemical alteration of the substratum, direct inhibition of settlement through the instability of the turf-sediment matrix, or via harbouring a larger number of micro-grazers within turfs that inhibit recruitment through increased grazing pressure on kelp recruits (Kennelly 1987; Vadas et al. 1992; Gorman and Connell 2009). Certainly, filamentous turf appears to thrive in the turf-sediment matrix, no doubt due to vegetative reproduction and the high light environment of areas devoid of kelp. The concern is that the positive feedback of both kelps and turfs implies threshold effects exist and the possibility that turf represents a degraded and alternative stable state.

Our results showed high rates of sediment deposition in PPB compared to other urbanised systems, e.g. Adelaide, Australia $10 - 622 \text{ g m}^{-2} \text{ d}^{-1}$ (Irving and Connell 2002a; Fernandes 2008; Fernandes et al. 2008), Italian Mediterranean $1.6 - 177.9 \text{ g m}^{-2} \text{ d}^{-1}$ (Airoidi et al. 1996; Airoidi and Virgilio 1998; Balata et al. 2005), and $1 - 8 \text{ g m}^{-2} \text{ d}^{-1}$ around the Kaikoura Peninsula on New Zealand's South Island (Schiel et al. 2006). Also, seasonal sediment deposition in kelp beds was elevated compared to habitat devoid of kelp. Overlap in the periods of seasonally high sediment deposition and the timing of early life-history process for *E. radiata* is likely to impact settlement of spores, growth of gametophytes, and sexual reproduction (Watanabe et al. 2016). Therefore, I predicted that sediments would impact *E. radiata* recruitment and algal community structure, but since no *E. radiata* recruited to the panels, I have no experimental data on the effect of sediments on *E. radiata*.

I also found little evidence that sediment deposition up to double the observed natural rates influenced algal community structure on the panels. Nevertheless, cover of encrusting coralline algae almost doubled under elevated sedimentation in the southeast, which may be a response to shading caused by a sediment layer. While there was one outlier, the general findings of nil impact of enhanced sedimentation contradicts a large body of literature that report significant direct and indirect negative impacts of elevated sediments on temperate reef biota including macroalgae (Schiel et al. 2006; Strain et al. 2014; Strain et al. 2015). The observed variability in seasonal sediment deposition rates and the size spectra of depositing sediments suggests that both urchin barren and kelp bed communities on shallow reefs in PPB have likely developed sediment tolerant assemblages. Additionally, it seems probable that the action of water motion at the shallow depths of the study sites ameliorates negative impacts of sediment in the PPB system studied here.

Post-settlement processes

An important aspect of ecosystem stability is the capacity of component species to replenish once it has declined. Above I have discussed bottlenecks in the early life-stages of *E. radiata*, where recovery following a perturbation is limited by successful settlement of spores. However, another vital aspect of a kelp beds capacity to persist is the capacity to recover from events that cause acute (complete loss of an individual from a bed) or chronic (small reductions of biomass from an individual overtime) loss of biomass.

Maintenance of Ecklonia radiata populations: acute loss of Ecklonia radiata

Densities of *E. radiata* sporophytes in kelp beds in PPB are within the reported range of densities of this species elsewhere (2 – 45 individuals m⁻²) (Schiel and Choat 1980; Miller et

al. 2011). While other studies have reported consistency in *E. radiata* sporophyte density across large spatial scales (Wernberg 2009; Wernberg et al. 2010), PPB is distinguished by marked differences in *E. radiata* population stability, with declining populations in the southeast and north and a stable population in the southwest. Lack of population stability of *E. radiata*, suggests limited capacity to recover. Wernberg (2010) showed reduced resilience in *E. radiata* populations with increasing water temperatures reducing the density of recruits. Within the time frame of the current study the north and southeast regions of PPB showed considerable reduction in recruitment limiting their capacity to recover from significant reductions to the reproductive portion of the *E. radiata* population. All regions in PPB experienced significant increases in density of the sea urchin *H. erythrogramma*, in most cases higher than the threshold density of *H. erythrogramma* required to initiate destructive overgrazing in PPB (Kriegisch et al. 2016). The significant differences in regional persistence of *E. radiata* kelp beds in PPB correlate with abundances of the *H. erythrogramma*.

Survival of Ecklonia radiata depends on region, urchin biomass, or life-stage

I found that survival of *E. radiata* thalli depended on the region, with the lowest survival occurring in the southeast. Similarly, Hatcher et al. (1987) reported spatially dependent differences in survival of *E. radiata*, however, over much greater distances (400 km) than examined in PPB (100 km). In the current study, differences in survival among regions appear to be driven by differences in *Heliocidaris erythrogramma* biomass. The exception was high survival of transplanted *E. radiata* thalli in the western region where biomass of *H. erythrogramma* was high, but so was kelp survival. This difference in kelp survival could be related to regional differences in the size distribution of the urchins. Urchins in the southeast are large with high individual biomass compared to small urchins in the west. Hagen and

1652 Mann (1994); Dumont et al. (2004) found size specific aggregation and movement patterns in
 1653 the urchin *Strongylocentrotus droebachiensis*, with larger urchins more likely to aggregate
 1654 together and move over greater distances searching for food than smaller urchins, suggesting
 1655 greater likelihood of over grazing by large urchins. The greater impact of urchins in the
 1656 southeast could also relate to the relatively small size of *E. radiata* sporophytes in this region.
 1657 The smaller sizes of Stage III *E. radiata* in the southeast would result in an individual being
 1658 grazed faster for a given urchin biomass and size structure than the larger sporophytes at
 1659 other sites. Transplanting *E. radiata* thalli onto *H. erythrogramma* urchin barrens at ambient
 1660 urchin biomass resulted in low survival of all sporophyte life-stages. Interestingly, reducing
 1661 ambient *H. erythrogramma* by half increased the survival of *E. radiata* from 25% to 72%,
 1662 which is similar to the survival rates of unmanipulated *E. radiata* in kelp beds. Dean et al.
 1663 (1984) examined survival of sporophytes of *Macrocystis pyrifera* and *Pterygophora californica*
 1664 exposed to differing densities of the sea urchins *Strongylocentrotus franciscanus* and
 1665 *Lytechinus anamesus*, with both species of urchin, at high densities, causing decreased
 1666 survival of kelps. These findings suggest that lowering urchin biomass before transplanting
 1667 kelp sporophytes will increase the likelihood of success in rehabilitation of urchin barrens.

1668

1669 *Chronic drivers of kelp bed maintenance: biomass loss exceeds growth*

1670 Similar to many other studies, I observed clear seasonal and spatial patterns in biomass
 1671 accumulation rates of the kelp *E. radiata* (Kirkman 1984; Novaczek 1984; Kirkman 1989;
 1672 Miller et al. 2011), with the highest accumulation in spring and summer as identified in other
 1673 kelp species (Mann 1973; Johnson and Mann 1988; Krumhansl and Scheibling 2011). Erosion
 1674 rate was highly variable temporally and spatially, and was likely related to both biological and
 1675 physical drivers (Larkum 1986; Kirkman 1989; Krumhansl and Scheibling 2011; Miller et al.

2011). Other studies have identified physical drivers such as nutrient and light availability and wave exposure as important in driving biomass accumulation, while wave exposure, temperature, and biological drivers (e.g. the number of epiphytes and presence of grazers) are more commonly associated with elevated biomass loss rates (Johnson and Mann 1986; Krumhansl and Scheibling 2011). The net balance between rates of biomass accumulation and loss indicates whether a kelp bed is increasing or decreasing (Krumhansl and Scheibling 2011). Thus, the large negative net annual productivity values observed among sites in PPB are a result of large biomass loss rates and could be indicative of declining *E. radiata* populations in PPB over the observation period.

Conclusion

Our data indicate that the recovery potential of kelp beds in PPB is determined by the interplay of intrinsic and extrinsic factors. All adult *Ecklonia radiata* in PPB are fecund, but different regions show two-fold variability in kelp survivorship from estimated spore loading to appearance as a macroscopic sporophyte. The capacity for kelp bed recovery, therefore, appears to be determined by the interplay among those species present to occupy available space, the factors that confer a competitive advantage to taxa that recruit to that space, and the biomass of the grazing *H. erythrogramma*. *E. radiata* as newly-settled recruits appear to be poor competitors and are dependent on the direct influence of the adult portion of the population that act to reduce the competitive ability of other species (e.g. via decreased light and abrasion). Lack of the direct effect of physical influence from adult kelps appears to result in the breakdown of recovery potential, resulting in dominance by undesirable turfs, which in turn results in reducing successful recruitment of kelps. It is clear that recruitment represents a bottle-neck in the capacity for *E. radiata* to recover from loss of biomass and

1700 maintain stable kelp beds. Furthermore, high sea urchin abundance overwhelms any capacity
1701 to recover due to low survival of all sporophytes, particularly for early recruits. Reducing sea
1702 urchin numbers can increase the likelihood of kelp survival, which is particularly important
1703 for establishment of the early stage sporophytes and maintenance of reproductive adults
1704 critical for kelp bed resilience. More research is necessary to understand the extrinsic factors
1705 that may impact settlement of kelps. This study also emphasises the role that judicious
1706 management could play in maintaining key components that contribute to stability of kelp
1707 beds through 1) maintaining high propagule pressure, 2) reducing factors that confer
1708 competitive advantage to the turf sediment-matrix, and 3) reducing urchin biomass to
1709 increase the survival of recruiting sporophytes.

1710

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1982 Appendices

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1984 Appendix 1. Mean and standard deviation for depth, *Heliocidaris erythrogramma* and algal taxa abundance as
 1985 percent cover for the 4 experimental sites in Port Phillip Bay (west; north; southeast and southwest) and two
 1986 habitats (kelp bed and sea urchin barren).
 1987

a) Kelp-bed habitat

	north		southeast		southwest	
	Mean	SD	Mean	SD	Mean	SD
Depth	3.42	0.37	3.70	0.58	2.62	0.96
<i>Heliocidaris erythrogramma</i>	5.84	3.47	3.32	2.60	2.56	3.29
Canopy-formers						
<i>Ecklonia radiata</i>	76.2	24.30	36	13.48	40.44	36.41
<i>Sargassum vestitum</i>	7.44	10.81	7.48	7.12	12.36	16.60
<i>Acrocarpia paniculata</i>	0	0	1.12	2.27	0	0
<i>Sargassum decipiens</i>	0	0	0.98	2.31	0.48	1.05
<i>Cystophora moniliformis</i>	0.02	0.14	0.6	1.37	0.64	2.20
<i>Cystophora</i> spp	0.2	1.41	0.5	1.64	0	0
<i>Sargassum fallax</i>	0.02	0.14	0.14	0.35	0.36	1.04
<i>Hormosira banksii</i>	0	0	0.02	0.14	0	0
<i>Caulocystis</i> spp	0	0	0	0	1.8	2.84
<i>Undaria pinnatifida</i>	6.5	9.80	0	0	0	0
Understory						
Foliose browns	0	0	9.8	19.56	0	0
<i>Zonaria turneriana</i>	0.12	0.72	3.74	4.49	0.28	0.46
<i>Caulerpa geminata</i>	0.02	0.14	1.78	4.14	0.04	0.2
<i>Exallosorus olsenii</i>	0	0	1.24	2.19	0.08	0.28
<i>Lenormandia marginata</i>	0.72	1.63	1.14	2.90	0	0
<i>Caulerpa longifolia</i>	0	0	0.94	2.90	0	0
<i>Lobospira bicuspidata</i>	0	0	0.9	3.01	0	0
<i>Caulerpa remotifolia</i>	0	0	0.6	1.58	0.76	1.36
<i>Distromium flabellatum</i>	0	0	0.58	1.37	0	0
<i>Dictyota dichotoma</i>	0.02	0.14	0.48	1.03	0	0
<i>Caulerpa</i> spp	0	0	0.14	0.40	0.4	2
<i>Lobophora variegata</i>	0	0	0.06	0.24	0	0
<i>Caulerpa simpliciuscula</i>	0	0	0.06	0.24	0	0
Foliose coralline red	1.22	4.11	0.06	0.24	0	0
<i>Dictyomenia</i> sp	0	0	0.06	0.24	0.04	0.2
<i>Dilophus marginatus</i>	0	0	0.02	0.14	0	0
<i>Botryocladia sonderi</i>	0	0	0.02	0.14	0.16	0.37
Foliose greens	0	0	0	0	0.28	1.02
Foliose reds	0	0	0	0	5.6	8.21
<i>Stenogramme interrupta</i>	1	2.39	0	0	0	0
<i>Lenormandia marginata</i>	0.2	0.76	0	0	0	0

Turf						
Turf sediment-matrix	4.5	10.32	48.5	33.06	2	4.13
Red turf	0	0	6.82	12.96	0	0
Ephemeral						
Filamentous red	7.18	10.85	8.38	12.87	0.6	3
Brown filamentous	0	0	2.6	5.65	0	0
Epiphytic red	0	0	1.2	3.43	0	0
Ectocarpales spp	0.02	0.14	0.64	1.64	0	0
Filamentous green	0.04	0.20	0.58	1.37	0	0
<i>Ulva</i> spp	0.22	0.42	0.42	0.81	0.28	1.02
<i>Colpomenia sinuosa</i>	0	0	0.36	0.48	0	0
<i>Cladosiphon filum</i>	0	0	0.04	0.20	0.04	0.2
<i>Codium fragile</i>	0	0	0.04	0.20	0	0
Epiphytic brown	0	0	0.02	0.14	0	0
<i>Asperococcus bullosus</i>	0	0	0.02	0.14	0	0
<i>Codium</i> spp	0	0	0	0	0.08	0.28
Coralline algae						
Encrusting red coralline	73.9	24.42	4.06	5.82	3.32	9.42
<i>Corallina</i> spp	0	0	0	0	3.32	6.85

b *Heliocidaris erythrogramma* barren

	west		north		southeast		southwest	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Depth	2.32	0.18	3.25	0.32	5.15	0.78	2.81	0.17
<i>Heliocidaris erythrogramma</i>	19.84	19.27	3.12	2.88	3.04	2.58	4.68	4.63

Canopy-formers								
<i>Sargassum vestitum</i>	0	0	0.14	0.35	7.14	11.75	0	0
<i>Ecklonia radiata</i>	0	0	0.1	0.71	3.58	8.38	0	0
<i>Cystophora</i> spp	0	0	0.04	0.20	0.3	0.93	0	0
<i>Acrocarpia paniculata</i>	0	0	0	0	0.22	0.76	0	0
<i>Cystophora moniliformis</i>	0	0	0	0	0	0	0.08	0.28
<i>Sargassum fallax</i>	0	0	0	0	0	0	28.32	26.52
<i>Undaria pinnatifida</i>	7.7	18.53	4.94	6.38	0	0	0	0

Understory								
<i>Exallosorus olsenii</i>	0	0	0	0	1.52	7.04	0	0
<i>Dictyota dichotoma</i>	0.06	0.24	1.6	2.90	1.18	1.91	0	0
<i>Dilophus marginatus</i>	0	0	1.78	3.86	1.1	7.06	0	0
Foliose red	0.14	0.73	0.82	3.02	0.58	3.53	8.48	6.47
<i>Caulerpa remotifolia</i>	0.04	0.20	0.16	0.74	0.16	0.37	0.04	0.2
<i>Caulerpa geminata</i>	0	0	2.72	13.84	0.14	0.35	0	0
Foliose greens	0	0	0.04	0.20	0.14	0.35	0	0
<i>Distromium flabellatum</i>	0	0	0	0	0.04	0.20	0	0
<i>Lobophora variegata</i>	0	0	0	0	0.02	0.14	0	0
<i>Zonaria turneriana</i>	0	0	0	0	0.02	0.14	0	0
<i>Caulerpa longifolia</i>	0	0	0	0	0.02	0.14	0	0
<i>Dictyoptis muelleri</i>	0	0	0.2	0.99	0	0	0	0

<i>Caulerpa</i> spp	0	0	0.02	0.14	0	0	0	0
Foliose coralline red	0	0	0.16	0.37	0	0	0.08	0.28
<i>Botryocladia sonderi</i>	0.04	0.20	0	0	0	0	0	0
<i>Gracilaria</i> spp	0.4	1.03	0.04	0.20	0	0	0	0
Foliose browns	0.5	3.54	0.02	0.14	0	0	0.08	0.28
Turf								
Turf-sediment matrix	9.9	17.36	48.50	37.84	28.10	28.80	25.80	26.17
Red turf	0	0	0	0	0	0	8.4	8.63
Ephemeral								
Cyanobacteria	0	0	0	0	1.32	4.21	0	0
Filamentous red	0.56	3.54	0	0	0.46	0.81	0	0
Filamentous brown	10.38	19.93	17.2	29.08	0.24	0.43	0	0
Filamentous green	0.96	3.68	0.08	0.27	0.24	0.43	0.2	1
<i>Ulva</i> spp	3.24	5.80	0.16	0.37	0.06	0.24	6.8	11.35
Epiphytic brown	0.5	3.54	0	0	0	0	0	0
<i>Cladosiphon filum</i>	0	0	0.76	1.00	0	0	0	0
<i>Colpomenia sinuosa</i>	0.02	0.14	1.1	1.83	0	0	0.16	0.37
Ectocarpales spp	0	0	0	0	0	0	3.6	5.11
<i>Codium</i> spp	0	0	0.06	0.24	0	0	0.48	2.00
Epiphytic foliose red	0.5	3.54	0	0	0	0	0	0
Coralline algae								
Encrusting red corallines	6.36	13.74	2.28	7.95	4.14	7.19	0.60	0.50

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2013 Appendix 2. Results of logistic regression model selection comparing the effects of (a) Site (west, north,
 2014 southeast and southwest), Treatment (4 levels: kelp-bed, procedural control, ambient and reduced sea-urchin
 2015 biomass on barren habitat) and life-stage (3 levels: Stage I, Stage II and Stage III) on the survival of *Ecklonia*
 2016 *radiata*. The best overall model is highlighted in bold.

Model No	Model	df	AICc	ΔAIC	LogLikelihood	Rank
1	SitexTreatmentxLife-stage	39	2036.9	1961.81	-784.45	12
2	SitexTreatment+Life-stage	15	86.59	11.5	-20.8	4
3	Site+TreatmentxLife-stage	15	94.84	19.75	-24.92	5
4	SitexLife-stage+Treatment	15	86.03	10.94	-20.52	3
5	Site + Treatment + Life-stage	9	75.09	0	-26.18	1
6	Site + Treatment	7	78.06	2.96	-30.63	2
7	Site +Life-stage	6	110.84	35.75	-48.4	8
8	Treatment + Life-stage	6	108.34	33.24	-47.14	6
9	Life-stage	3	132.66	57.56	-63.05	11
10	Treatment	4	109.05	33.96	-50.06	7
11	Site	4	111.41	36.32	-51.24	9
12	Null(intercept)	1	132.62	57.52	-65.27	10

2017 Appendix 3. Results of logistic regression model selection comparing the effects of (a) Site (north, southeast and
 2018 southwest), Taxa (2 levels: kelp and fucoid) and life-stage (2 levels: juvenile i.e. non-reproductive individuals and
 2019 adults reproductive sporophytes) on the likelihood of finding sporophytes attached to stable vs. unstable
 2020 substrates. The best overall model is highlighted in bold.
 2021

Model No	Model	df	AIC	ΔAIC	LogLikelihood	Rank
1	SitexTaxaxLife-stage	12	43.35	4.37	-9.67	5
2	SitexTaxa+Life-stage	7	38.97	0	-12.49	1
3	Site+TaxaxLife-stage	6	41.12	2.14	-14.56	4
4	SitexLife-stage+Taxa	7	40.3	1.33	-13.15	3
5	Site + Taxa + Life-stage	5	39.46	0.48	-14.73	2
6	Site + Taxa	4	58.32	19.34	-25.16	7
7	Site +Life-stage	4	55.58	16.6	-23.79	6
8	Taxa + Life-stage	3	59.74	20.77	-26.87	8
9	Life-stage	2	83	44.03	-39.5	9
10	Taxa	2	92.19	53.21	-44.09	10
11	Site	3	103.83	64.85	-48.91	11
12	Null(intercept)	1	166.62	127.65	-82.31	12

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2042 CHAPTER 3: Reduced resistance to sediment-
2043 trapping turfs with decline of native kelp and
2044 establishment of an exotic kelp
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Abstract

Understanding the strength and direction of interactions among species is vital to anticipate how ecosystems will respond to ongoing anthropogenic stressors. Here we examine the ecological function of native (*Ecklonia radiata*) and invasive (*Undaria pinnatifida*) kelps in resisting domination by sediment-trapping turf on reefs within the highly urbanised Port Phillip Bay (PPB), Australia. Short-term (30 days) and long-term (740 days) manipulations demonstrated that kelp laminae can clear and maintain the substratum free of turfs, while conversely, removal of kelp leads to a proliferation of sediment-trapping turfs. Analyses looking at the relationship between total length of *E. radiata* and *U. pinnatifida* and the area cleared of turf algae showed the per capita clearing effect of *E. radiata* over a year was ~1.7 times greater than that of *U. pinnatifida* due to the annual die-back of the invasive. A natural experiment identified that ongoing sea urchin (*Heliocidaris erythrogramma*) grazing lead to native kelp bed decline, facilitating turf dominance. Even though *U. pinnatifida* establishes once native beds are disturbed, its ecological function in clearing turf is weaker than *E. radiata*, given its annual habit. It seems apparent that turfs represent the more persistent and problematic algal group dominating temperate reefs in PPB, and are likely changing the structure, function and energy flows of shallow temperate reefs in this urbanised estuary.

Introduction

Interspecific interactions among plants and animals ultimately underpins the structure and dynamics of communities and whole ecosystems (Hambäck and Beckerman 2003; Brooker 2006). Local-scale interactions among species can create well-defined ‘emergent’ patterns that remain consistent over large spatial scales (Paine 1984; Dayton 1985; Fowler-Walker and Connell 2002). However, in the face of accelerating anthropogenic stressors (non-native species introductions, fishing pressure, ocean acidification, nutrification, and sedimentation), previously well-understood biotic interactions and emergent ecological dynamics may be altered, and thus require reappraisal. A key challenge lies in understanding how continuing anthropogenic impacts may alter the relative importance of biotic interactions or create entirely novel interactions that modify patterns in the distribution and abundance of critical species.

Kelps commonly refer to the orders Laminariales and Fucales and are considered foundation species (sensu Dayton 1972) of shallow temperate reef ecosystems, as they provide much of the three-dimensional habitat structure, standing biomass and food for associated species (Dayton 1985; Ling 2008; Schiel and Lilley 2011; Steneck and Johnson 2014). As biogenic habitats, kelp beds also influence local environmental factors such as water motion (Eckman et al. 1989; Jackson 1997; Wernberg et al. 2005), light (Kennelly 1989; Connell 2003a; Wernberg et al. 2005), sediment accumulation (Eckman et al. 1989; Wernberg et al. 2005), and pH (Hofmann et al. 2011; Roleda et al. 2015; Britton et al. 2016).

The kelp *Ecklonia radiata* is the single most important foundation species on southern Australian sub-tidal reefs, exerting a strong structuring effect on the benthos. Shading and

2100 abrasion by *E. radiata* results in a clearing effect that negatively influences sessile
 2101 invertebrates (Connell 2003b; Goodsell et al. 2004) and understory algae (Kennelly 1989;
 2102 Goodsell et al. 2004; Bennett and Wernberg 2014), and this clearing effect acts to control
 2103 normally subordinate algal species such as sediment-trapping turfs (Connell 2003a; Gorgula
 2104 and Connell 2004; Wernberg et al. 2016) and invasion by non-native algae (i.e. *Undaria*
 2105 *pinnatifida*) (Valentine and Johnson 2003; Carnell and Keough 2014). Conversely, the removal
 2106 of adult *E. radiata* individuals eliminates the negative effects of *E. radiata* on understory taxa,
 2107 and can result in uptake of space by sediment-trapping turfs (Kennelly 1987a; Gorgula and
 2108 Connell 2004; Wernberg et al. 2016) that can act to reduce available safe sites (microsites
 2109 suitable for recruitment, development and establishment – sensu Harper, 1967) for early life-
 2110 stages of kelp, through competition (Kennelly 1987a; Connell 2003a) or chemical alteration of
 2111 benthic substrata (Kennelly 1987a). On coastlines adjacent to growing human populations,
 2112 localised anthropogenic inputs (enhanced nutrient and sediment loading) can alter the
 2113 interaction strengths between normally subordinate turfs and the dominant *E. radiata*
 2114 (Gorgula and Connell 2004; Connell et al. 2008), resulting in decline and loss of *E. radiata*
 2115 kelp beds (Connell et al. 2008; Gorman and Connell 2009). Similar phenomena have been
 2116 reported elsewhere around the world for other large canopy-forming brown algae in the
 2117 Laminariales and Fucales (Airoldi and Cinelli 1997; Eriksson 2002; Perkol-Finkel and Airoldi
 2118 2010; Moy and Christie 2012; Campbell et al. 2014; Strain et al. 2014; Krumhansl et al. 2016).
 2119 Shifts from kelps to turfs have broad implications for temperate reefs and kelp resilience via
 2120 reduction in kelp recruitment, primary productivity and habitat structure (Kennelly 1987a;
 2121 Copertino et al. 2005; Christie et al. 2009; Moy and Christie 2012). Most importantly systems
 2122 dominated by turfs are perceived to be of less value to human societies than the kelps they
 2123 replaced, making prevention of such shifts beneficial from both ecological and socio-

2124 economic perspectives (Falkenberg et al. 2015; Bennett et al. 2016; Filbee-Dexter and
 2125 Wernberg 2018).
 2126
 2127 Declines in native algal species can also facilitate establishment of invasive macroalgae. The
 2128 kelp *Undaria pinnatifida* (Harvey) Suringar is considered one of the world's most invasive
 2129 species, increasing its range over much of the temperate zone over the last 30 years
 2130 (Sanderson 1990; Hay and Villouta 1993; Campbell and Burridge 1998; Curiel et al. 1998;
 2131 Valentine and Johnson 2003; Thornber et al. 2004; Irigoyen et al. 2011; Epstein and Smale
 2132 2017). There is increasing recognition that *U. pinnatifida* is a passenger and not a driver
 2133 (sensu MacDougall and Turkington 2005) of ecological change (South and Thomsen 2016,
 2134 Valentine and Johnson 2003, 2004) in that it requires disturbance to free resources (space,
 2135 light, nutrients) and facilitate its establishment and growth (MacDougall and Turkington
 2136 2005). Several studies have reported positive benefits to recipient and nearby ecosystems
 2137 from *U. pinnatifida* via enhancement of nearshore productivity (Suárez-Jiménez et al. 2015a;
 2138 Tait et al. 2015; Epstein and Smale 2017) and providing cross-system subsidies (Suárez-
 2139 Jiménez et al. 2015b; Epstein and Smale 2017; South et al. 2017). In recent decades, *U.*
 2140 *pinnatifida* has established extensive self-sustaining populations in both Victoria and
 2141 Tasmania (Sanderson 1990; Campbell and Burridge 1998), coincident with declines in native
 2142 kelp such as *E. radiata* (Valentine and Johnson 2003; Carnell and Keough 2014).
 2143
 2144 In this study, we assess whether the invasive *U. pinnatifida* is capable of fulfilling a similar
 2145 'turf clearing' ecological function to that of *E. radiata* in a large urbanised embayment in
 2146 southeast Australia (Port Phillip Bay) where *E. radiata* is declining while the exotic kelp is
 2147 spreading (Primo et al. 2010; Jung et al. 2011; Crockett et al. 2017). We used a series of

- 2148 manipulative and natural field experiments, spanning two years, and surveys to establish the
- 2149 capacity of a native and invasive kelp (*Ecklonia radiata* vs. *Undaria pinnatifida*) to
- 2150 mechanically clear and prevent sediment-trapping turfs from overgrowing rocky reef.
- 2151

Materials and Methods

Study site

This research was undertaken on rocky reef in the north of Port Phillip Bay (PPB), adjacent to Williamstown Beach (hereafter Williamstown; S 37° 52' 10.5564", E 144° 53' 36.4884"), 10 km from the urban centre of Melbourne, Australia (population ~5M; Fig 1a). The Williamstown reef is contiguous from mean low water (MLW) to 5 m depth (width 150-200 m from MLW) where it grades to silty sand. The reef is conglomerate boulder and cobble basaltic rock (Bowler 1966), interspersed with small patches of sand (Fig 1b). Native kelp *Ecklonia radiata* [(C. Agardh) J. Agardh 1848, Family: Lessoniaceae] occurs as small remnant beds ($10 - 10^3 \text{ m}^2$) (Fig. 1b). The introduced annual Japanese kelp *Undaria pinnatifida* [(Harvey) Suringar, 1873, Family: Alariaceae] also occurs as small dense stands forming a closed canopy (typically covering ~0.5–1 m^2 with 4-20 individuals per patch). *U. pinnatifida* occurs as large ephemeral beds in the west of PPB where the invasive first established in PPB (circa 1996) (Campbell and BurrIDGE 1998). Turfing algae manifests in PPB as an epilithic-algal-sediment matrix, hereafter termed turf, composed of fleshy filamentous mixed Rhodophyta, Chlorophyta and Ochrophyta taxa that trap sediments to form a cohesive semi-consolidated matrix on the reefs, and is distinguished from filamentous algae lacking bound sediments or those comprised of articulated coralline algae (e.g. Connell 2003). The Williamstown reef is dominated by the sea urchin *Heliocidaris erythrogramma* (Valenciennes, 1846; Family: Echinometridae), which forms and maintains sea urchin barrens (Fig. 1b). The urchin barrens are characterised by bare-rock and/or high cover of encrusting non-geniculate corallines and turf algae that form a continuous network among the remnant beds of *E. radiata*.

2177 Under low water-motion both *Ecklonia radiata* and *Undaria pinnatifida* stand erect on thick
2178 stipes, however, in surge the flexible sporophytes sway back and forth to radially sweep the
2179 surrounding benthos – termed the whiplash effect (Dayton 1975). *U. pinnatifida*, unlike the
2180 perennial *E. radiata*, is an annual kelp and in Australia it has a winter (July – October) growing
2181 period followed by senescence of the blade in spring through summer (September –
2182 January). For this reason, short-term experiments (Exp. 1 and 2) of 30 days were established
2183 to contrast the two kelps at a time coinciding with maximal blade length of *U. pinnatifida*
2184 (August –September).

2185

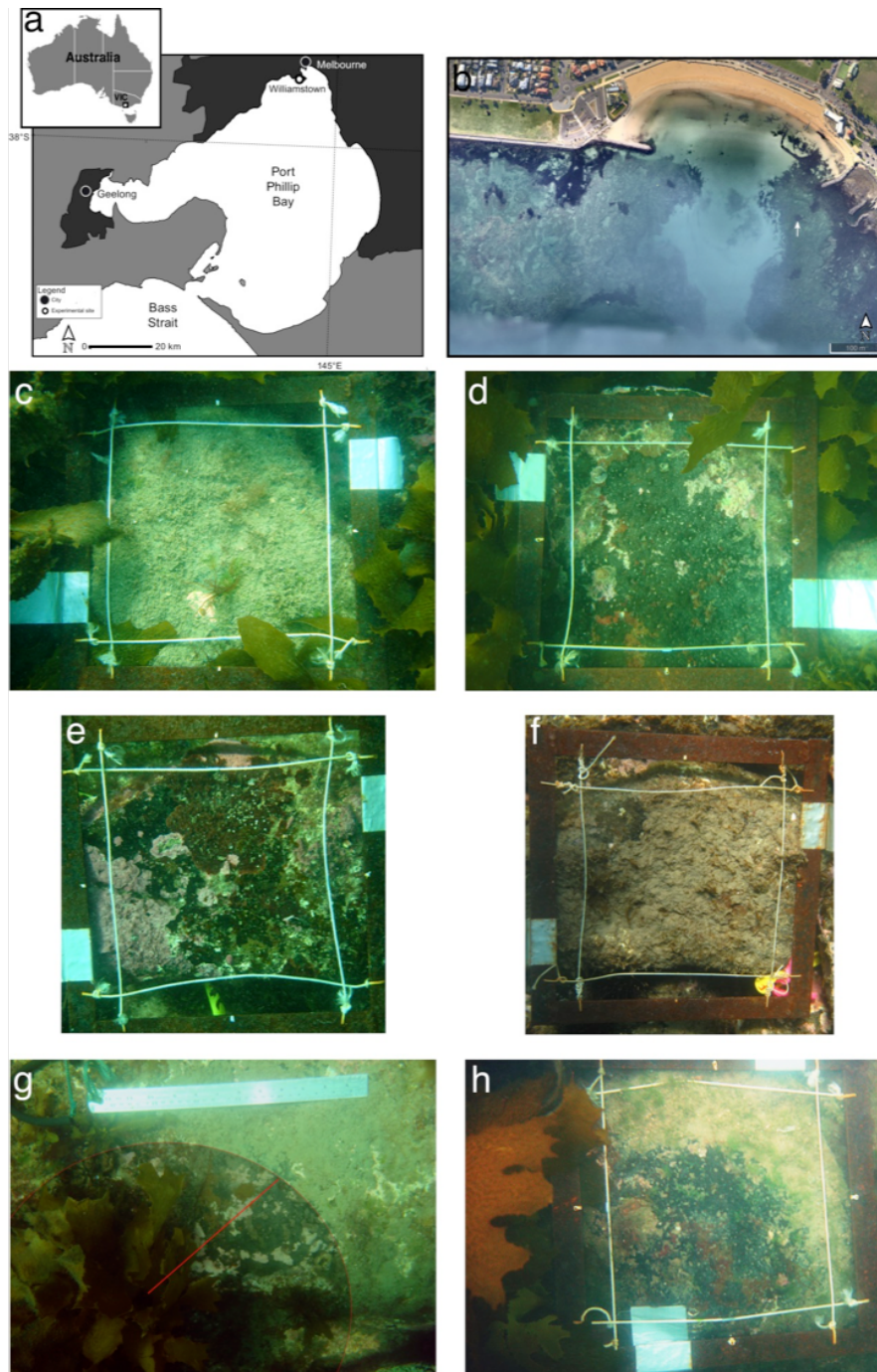


Figure 1 a) Map of Port Phillip Bay, an urbanised embayment in south-eastern Australia. Major cities (large symbols, bounded in white) and the study site at Williamstown (small white symbol, bounded in black) are shown; b) The Williamstown study site, showing remnant kelp-beds (as dark patches) surrounded by urchin barrens (mottled), and grading to silty sand. The white arrow indicates the remnant kelp-bed where the experiment was located. c) Initial cover of sediment-laden turf matrix in a 'Turf to kelp' plot; d) the same 'Turf to kelp' plot at 1 month; e) a 'Kelp cleared' plot showing the benthic assemblage after clearing of kelp, note the cover of pink encrusting coralline algae and lack of any turf-sediment matrix; f) the build-up of turf in the same 'Kelp removed' plot 10 months after kelp removal; g) the maximal radius of influence of an individual kelp thallus (red arrow; note: this was measured in-situ not estimated from photos) used to calculate the area of scour influence (shaded area); h) a 'Turf to kelp' plot where the effect of the kelp clearing turf has been ameliorated by sea urchin overgrazing of the kelps, a partial clearing effect is still observable as a scar in the turf in the lower left corner.

2199 *Experiment 1: Effect of native and invasive kelp on sediment-trapping turf*

2200 To test the effect of kelp on turf, 16 flat rocks (eight for *E. radiata* treatments and eight for *U.*
 2201 *pinnatifida*, of mean planar surface area $0.084 \pm 0.006 \text{ m}^2$) with 100% cover of turf (mean turf
 2202 depth of $12.45 \pm 4.09 \text{ mm}$; see Fig. 1c) were harvested from the study site and transplanted
 2203 from open turf dominated reef at 2-3 m depth to an adjacent reef platform at the same
 2204 depth. four turf-covered rocks were placed nestled within the reef substrata to be flush with
 2205 the surrounding reef and within the maximum radial extent of five *E. radiata* thalli, while
 2206 another four were moved within the radial extent of *U. pinnatifida* (the 'turf-to-kelp'
 2207 treatment: $n=4$ for *E. radiata* and $n=4$ for *U. pinnatifida*). These rocks were placed to not be
 2208 permanently covered by the kelp canopy under calm conditions, but to be within the
 2209 maximal reach of the kelp laminae under conditions of elevated water motion.

2210 A further eight turf covered rocks were harvested from the study site and placed nestled
 2211 within the reef substrata to be flush with surrounding reef within a kelp free area of the reef,
 2212 i.e. greater than 1 m distant from any kelp thalli (the 'Turf to no kelp', $n=4$ for *E. radiata* and
 2213 $n=4$ for *U. pinnatifida*). All rocks were placed $\geq 1 \text{ m}$ apart from other experimental rocks to
 2214 ensure independence of treatments, and all were at a similar depth ($2.3 \pm 0.18 \text{ m}$)

2215 *Experiment 2: Effect of native and invasive kelp removal on sediment-trapping turf*

2216 *development*

2217 16 flat rocks with 100% kelp canopy cover (~five mature sporophytes on replicates rocks of
 2218 mean planar surface area $0.084 \pm 0.006 \text{ m}^2$) of *E. radiata* ($n=8$) or *U. pinnatifida* ($n=8$), were
 2219 harvested from the study site and transplanted from kelp beds into an opening in the kelp

2220 bed adjacent to the treatments for Exp. 1 and held within the reef substrata to be flush with
 2221 the surrounding reef. Eight of the replicates were cleared of kelp canopy by complete
 2222 removal of all kelp individuals including the holdfast (i.e. 'kelp-removed' treatment, n=4 for *E.*
 2223 *radiata* and n=4 for *U. pinnatifida*; see Fig. 1e), while the kelp on the remaining eight rocks
 2224 were not manipulated acting as a control (i.e. 'kelp-not-removed' treatment, n=4 for *E.*
 2225 *radiata* and n=4 for *U. pinnatifida*).

2226 For Expts. 1 & 2 the effect of kelps and kelp removal on planar percentage cover of turf,
 2227 encrusting coralline algae (ECA) and counts of recruited kelps were assessed. A 0.2 x 0.2 m
 2228 quadrat was placed in the centre of replicate rocks to provide a standardised area for
 2229 estimating planar percentage cover of turf, encrusting coralline algae (ECA), and to count any
 2230 recruited kelps. To aid consistent placement of the quadrat, two plastic locating pegs were
 2231 secured on either side of each replicate to ensure repeated sampling of the same central 0.2
 2232 x 0.2 m area. Percentage cover was assessed from photographs taken on SCUBA using the 0.2
 2233 x 0.2 m quadrat, all photos were calibrated and analysed in ImageJ (Schneider et al. 2012)
 2234 and recruited kelps were counted insitu. The effects of both kelps on percent cover of turf
 2235 were contrasted at 30 days using two-way ANOVA (for Exp. 1. fixed treatment effects were
 2236 kelp presence and kelp species. For Exp. 2 fixed treatment effects were kelp removal and kelp
 2237 species). *E. radiata* treatments for Exp. 1 and 2 were continued and assessed every 2-3
 2238 months up to 12 months and analysed using 1-way analysis of variance (ANOVA) at the final
 2239 sample date (February 2013) (fixed effect treatment = presence / absence of *E. radiata*).
 2240 Additionally, the effect of *E. radiata* on the proliferation of *U. pinnatifida* was also analysed at
 2241 the peak of *U. pinnatifida* abundance (October 2012).

2242

2243 *A natural experiment examining the effect of invasion by urchins*

2244 Sea urchins (*Heliocidaris erythrogramma*) were monitored within a 0.25 x 0.25 m quadrat
 2245 centered on all experimental rocks (i.e. an additional 5 cm on each dimension beyond the
 2246 central 0.20 x 0.20 m quadrat for assessing algal composition). Kelp cover was also monitored
 2247 in the ‘turf-to-kelp’ and ‘kelp control’ treatments for the duration of both Exp. 1 and 2. We
 2248 chose not to maintain the experiment free of urchins, as we were interested in observing
 2249 natural dynamics. At ~12 months (February 2013) urchin density increased dramatically and
 2250 the *E. radiata* forming treatments began to decline (Blue arrow Fig. 4 and 5). Hereafter, the
 2251 *E. radiata* experimental treatments were pooled and replaced by a natural experiment that
 2252 enabled inferences on the effects of invasion by urchins on turf and ECA cover. Experimental
 2253 plots for the natural experiment were accessed every 5 – 6 months to 28 months (2.3 years)
 2254 after initiating the experiments. Thus, the natural experiment was analysed at two years
 2255 assessing differences in turf and ECA cover.

2256 There was no need to establish a control to examine the effect of handling the rocks because
 2257 ‘turf’ and ‘kelp’ rocks were treated identically during the transplant process, i.e. all ‘turf’ and
 2258 ‘kelp’ rocks were lifted from the turf or kelp beds and moved a similar short distance. Thus,
 2259 any effects of the transplant process were consistent across all treatments. We contrasted
 2260 kelp cover between the two kelp treatments from Exp. 1. and Exp. 2. (i.e. ‘turf-to-kelp’ and
 2261 ‘kelp control’) as this enabled a comparison of transplanted kelps and un-transplanted kelps
 2262 acting as a handling control. Treatments with kelp showed similar kelp cover at all times
 2263 across experiments (Fig 5b).

2264 *Comparison of turf clearance function between invasive and native kelps*

2265 We measured the extent of kelp clearing turf for both the native and invasive kelp species by
2266 assessing the maximal radial extent of visible influence ('area of influence') of an individual
2267 kelp sporophyte (separate to the kelp bed) on surrounding turf (Fig. 1b and g) in depths of 2
2268 – 5 m on the Williamstown reef adjacent to Experiments 1 & 2. The area of influence of the
2269 individual kelps on surrounding turf and total kelp length (from the bottom of the stipe to tip
2270 of lamina) was determined for 80 haphazardly surveyed *E. radiata* and 80 *U. pinnatifida*
2271 individuals. The effect of native *versus* non-native kelp on the 'area of influence' (see Fig. 1g)
2272 on turf was compared using 1-way ANCOVA, with total kelp length as the covariate. For both
2273 kelps, we checked for linearity in the diagnostic plots of residual versus fitted values before
2274 describing the linear relationship between total sporophyte length and 'area of sporophyte
2275 influence' (based on monthly measurements) to estimate the mean area of turf cleared by an
2276 individual kelp thallus over the period July 2013 – August 2014. We estimated the difference
2277 in annual per-capita clearing of turf by integrating under the curves of area-cleared *versus*
2278 time for both species using the spline integration method from the MESS package in R
2279 (Ekstrom 2014).

2280 All transplants and samplings involving *U. pinnatifida* were sanctioned by the Victorian
2281 government Department of Environment Land Water and Primary Industries under permit
2282 (permit number NP 239). Prior to all analyses, data were checked for conformity to
2283 assumptions of homoscedasticity and normality. Where data were heteroscedastic, the
2284 transformation to stabilise variances was determined by the relationship between group
2285 standard deviations and means, and/or the Box-Cox procedure within the MASS package in R
2286 (Venables and Ripley 2002). Where appropriate, multiple range tests were conducted using
2287 Tukey's honest significant difference test. All analyses were undertaken using the R package

version 3.1.2 (R Development Core Team 2015) running in RStudio version 1.0.136 (RStudio Team 2015).

Results

Experiment 1: Effect of native and invasive kelp on sediment-trapping turf

Within three days of moving rocks covered in turf to the vicinity of kelps, observable scour marks outlined the radial extent of laminae clearing turf on the rocks, and within the cleared sections all visible sediments and much of the turf had been swept away, often leaving only the axial filaments of the turf still attached to the rock (see Fig. 1d and h). At one month, the cover of turf on rocks translocated adjacent to *E. radiata* fronds was reduced from an initial cover of 96 ± 4 SE % to 29 ± 27 SE % (Fig. 2a, Table 1a, Fig. 1d). One month after moving rocks covered in turf to the vicinity of *U. pinnatifida* fronds, turf cover declined significantly (Fig. 2a, Table 1a) from initial cover of 100% to 59.3 ± 12.1 SE %, while control (Turf to no kelp) rocks away from the radial extent of kelp fronds maintained 100% cover of turf (Fig 2a).

At one-year post initiation (February 2013) of the experiment examining the effect of *E. radiata* on turfs, turf cover had recovered to 59%, although this was still significantly lower than on control rocks not subject to the presence of kelp (Fig 4a, 1-way ANOVA, $F_{1,6} = 6.473$, $P = 0.043$). After one year of the experiment, the ECA cover on rocks, subject to declining kelp, dropped to its original level and was not different to that on control rocks (1-way ANOVA, $F_{1,6} = 0.34$, $P = 0.55$ Fig. 4c and 4d).

2307

Experiment 2: Effect of native and invasive kelp removal on sediment-trapping turf

development

At 30 days after commencement of the experiment, rocks cleared of native kelp had developed a significantly greater cover of turf ('Kelp removed': 39.24 ± 9.28 SE %) than occurred on the control rocks supporting intact *E. radiata* sporophytes ('Kelp not removed': 10.68 ± 5.09 SE %) (Fig 2b, Table 1b, Fig. 1e and f). Similar to the response of turf following *E. radiata* removal, removal of *U. pinnatifida* sporophytes ('Kelp removed') also stimulated rapid establishment of turf to a mean cover of 98.51 ± 1.74 SE %, while treatments with intact *U. pinnatifida* ('Kelp not removed') cover had low cover of turf (6.38 ± 12.76 SE %) (Fig 1b, Table 1b).

2318

From one to six months, the cover of turf was stable across both 'Kelp removed' and 'Kelp not removed' treatments but one year after kelp clearance, turf had increased to more than 90% cover (Fig. 4b). At the commencement of the experiment, cover of ECA was similar on both the 'treatment' ('Kelp removed') and control ('Kelp not removed') rocks (Fig. 4d). The temporal pattern in ECA cover showed a progressive decline concomitant with overgrowth by turf (Fig. 4d). After one year of the experiment, both treatment and control rocks supported 100% cover of turf, which had completely overgrown the ECA reflecting declining kelp cover on rocks in the control treatment as a result of urchin overgrazing (Fig. 4d; see Fig. 1f).

2327

Between one (April 2012) and eight months (October 2012) following removal of *E. radiata* from the rocks there was a well-defined seasonal increase in cover of *U. pinnatifida*, which peaked at 75 ± 25 SE % in October 2012 (Fig. 5a; effect of *E. radiata* removal on *U. pinnatifida* cover, 1-way ANOVA, $F_{1,6} = 9.00$, $P = 0.024$). *U. pinnatifida* cover on these rocks reduced to zero by mid-summer (February 2013) with senescence of the sporophytes, and there was little recruitment in the subsequent two years (Fig 5a).

2334

2335 *Comparison of the turf clearance function between invasive and native kelps*

2336 A significant negative effect of kelp on turf was observed for both the native and introduced

2337 kelps (Fig. 2a, Table 1a). Local proliferation of sediment-trapping turf did not occur in the

2338 presence of intact kelp patches, whether invasive or native. Interestingly, it was notable that

2339 development of turf was significantly greater on rocks from which *U. pinnatifida* was2340 removed (92.13% cover) than on those from which *E. radiata* was removed (39.24% cover)

2341 over the same period (Fig. 2b, Table 1b).

2342

2343 Not surprisingly, the area of influence of kelp on turf increased significantly with thallus size

2344 (ANCOVA, $F_{1,157} = 8.85$, $P = 1.41e^{-15}$) and at similar rates for both *E. radiata* and *U. pinnatifida*2345 ($F_{1,156} = 0.0004$, $P = 0.98$), but for a given thallus length the area of clearance around native2346 kelps was significantly greater ($F_{1,156} = 17.49$, $P = 4.80e^{-05}$) than that of the non-native (Fig2347 3a). However, because *U. pinnatifida* grows to a greater length than *E. radiata* on

2348 Williamstown reefs, this kelp has the capacity to scour a greater area than the native (Fig 3b)

2349 on a per capita basis. *U. pinnatifida*, because of its annual life history, begins to senesce in2350 November to completely dieback by late February. In contrast, the perennial *E. radiata*

2351 affects a smaller area, but does so continuously throughout the year (Fig. 3b). The annual and

2352 perennial phenologies of these kelps have a large effect in determining the integrated annual

2353 area of influence of each kelp on the benthos, or the amount of space maintained free of turf

2354 surrounding each kelp. As such, *E. radiata* maintains an area clear of turf and sediment 1.692355 times greater per year than *U. pinnatifida* (Fig 3b).

2356

2357

2358 *A natural experiment examining the effect of invasion by urchins*

2359 Starting in Feb 2013 the temporal trend in cover of *E. radiata* (defining experimental

2360 treatments, i.e. 'turf to kelp' and 'kelp control' treatments) showed a distinct decline (Fig 5b).

2361 This decline in *E. radiata* correlated strongly with increased local abundances of the sea

2362 urchin *Heliocidaris erythrogramma* at the study site, with an approximate doubling of *H.*

2363 *erythrogramma* density across all treatments (Fig. 5c). From Feb 2013 to Dec 2013 turf cover

2364 increased across all treatments and by the conclusion of the experiment in August 2014 turf

2365 cover on all treatments had increased to match that of the control rocks from Exp. 1 ('Turf to

2366 no kelp' treatment, Figs. 4a and 4b). Additionally, ECA cover on all treatments also dropped

2367 to zero by August 2014 irregardless of the stating conditions of the treatments (Figs. 4c and

2368 4d).

2369

2370

2371 Table 1. Two-way analysis of variance testing (a) the presence of kelp ('Treatment – 2 levels: presence
 2372 *versus.* absence of kelp) and kelp species (*Ecklonia radiata versus. Undaria pinnatifida*) on cover of
 2373 turf (Experiment 1, both fixed effects); and (b) kelp removal ('Treatment – 2 levels: kelp removal
 2374 *versus* kelp presence) and kelp species (*E. radiata versus. U. pinnatifida*) on proliferation of turf
 2375 (Experiment 2, both fixed effects). Both experiments were analysed one month after commencement
 2376 of the experiments (determined *a priori*). Transformations are expressed regarding the raw variate Y .
 2377 Significant effects are indicated by asterisks, with $\bullet p>0.05<0.1$, $*p<0.05$, $**p<0.01$, $***p<0.001$.
 2378

(a) Experiment 1 (transformation = $Y^{0.50}$)

Source	MS	F
Treatment	1.98E+08	58.74***
Species	9.58E+06	2.84
Treatment * Species	3.91E+06	1.16
Residuals	4.05E+07	

(b) Experiment 2 (transformation = $Y^{0.55}$)

Source	MS	F
Treatment	225.66	52.84***
Species	13.12	3.07
Treatment*Species	43.09	10.09**
Residuals	4.27	

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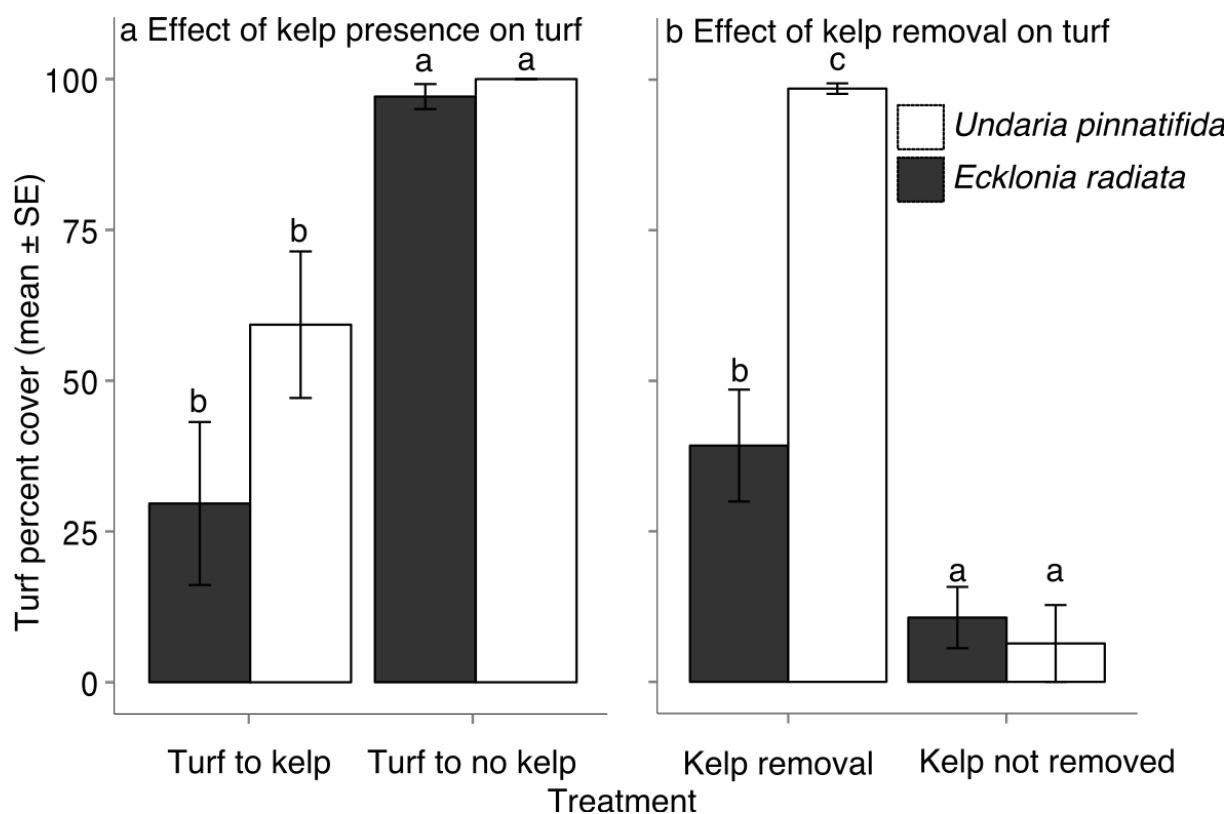


Figure 2 (a) The effect of kelp presence (Turf rocks transplanted next to kelp – ‘Turf to kelp’, $n=4$) and absence (Turf rocks transplanted to open reef – ‘Turf to no kelp’, $n=4$), and the identity of the kelp species (*Ecklonia radiata* as filled bars and *Undaria pinnatifida* as open bars) on cover of turf after 30 days; highest order significant term ‘Treatment’- $F_{1,12} = 58.74$, $P = 5.82e-7$. (b) The effect of kelp removal from rocks (Kelp removal, $n=4$) versus kelp present on rocks (Kelp not removed, $n=4$) and kelp species identity (as for 6a) on cover of turf after 30 days; highest order significant term ‘Treatment*Species’- $F_{1,12} = 10.09$, $P = 0.008$. Letters above each bar indicate significant Tukey’s groupings.

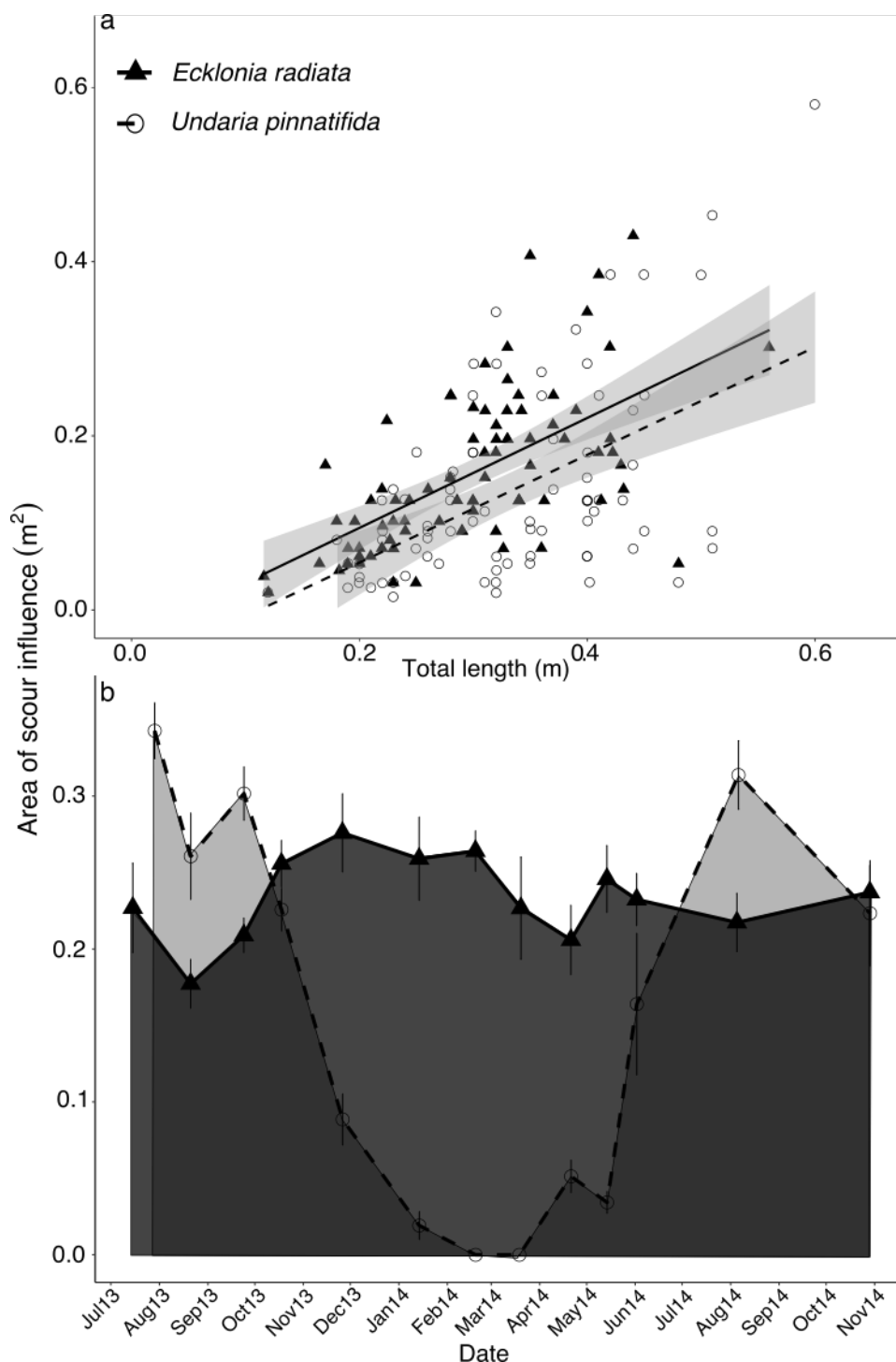


Figure 3 a) Relationship between total thallus length (m) and the per capita area of scour influence (m²) of kelp thalli on turf for native *Ecklonia radiata* (filled triangles, solid line) and invasive kelp *Undaria pinnatifida* (open circles, dashed line) using estimates from the ANCOVA model with values expressed on untransformed axes; n=80 thalli for each species, as measured at Williamstown during August – September 2014. b) Cleared area free of turf per adult sporophyte projected over 18 months (July 2013 to Nov 2014) as estimated from linear models for *E. radiata* $y = 0.63(x) + 0.032$, $r^2 = 0.36$, $P = 3.50 \times 10^{-9}$ (triangles and grey polygon, n=6 per month) and *U. pinnatifida* $y = 0.62(x) + 0.07$, $r^2 = 0.27$, $P = 5.2 \times 10^{-7}$ (circles, and black polygon, n=6 per month) (mean \pm SE).

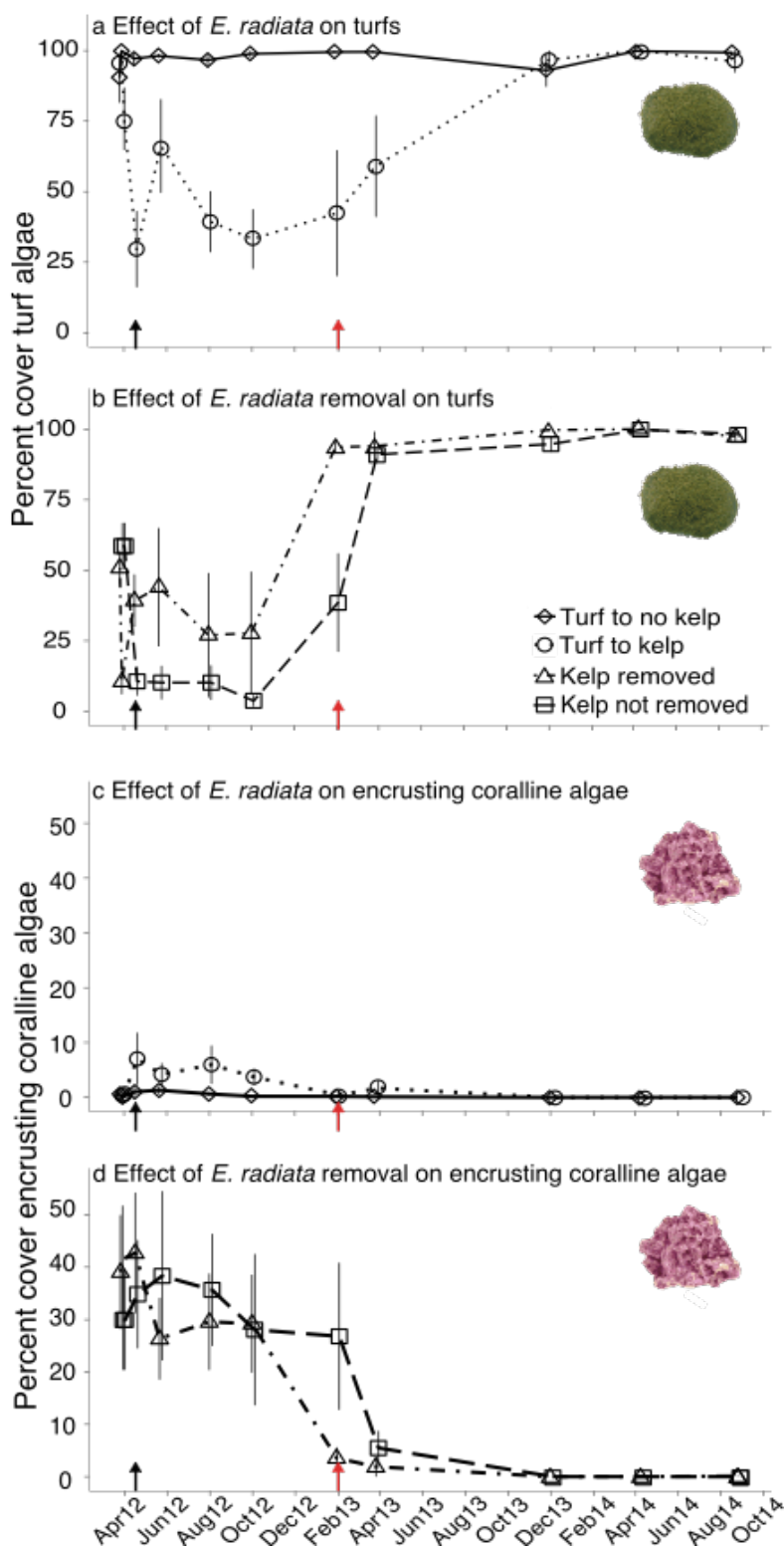


Figure 4 Percentage cover (mean \pm SE) of turf algae (panels a & b) and encrusting coralline algae (ECA) (panels c & d) in the presence and absence of the native kelp *Ecklonia radiata*. Panels a) and c) correspond to a long-term experiment (Exp. 4) examining the effect of kelp presence (Turf to kelp, $n=4$) versus kelp absence (Turf to no kelp, $n=4$). Panels b) and d) correspond to a long-term experiment (Exp. 5) detailing the effect of kelp removal from rocks initially dominated by *E. radiata* (Kelp cleared, $n=4$) versus intact kelp (Kelp not removed, $n=4$). The experiment was run for 840 days from March 2012 to October 2014. The black arrow indicates 30-day sampling for Expts. 1 and 2, red arrow indicates end of Expts. 1 and 2 and the start of the natural experiment.

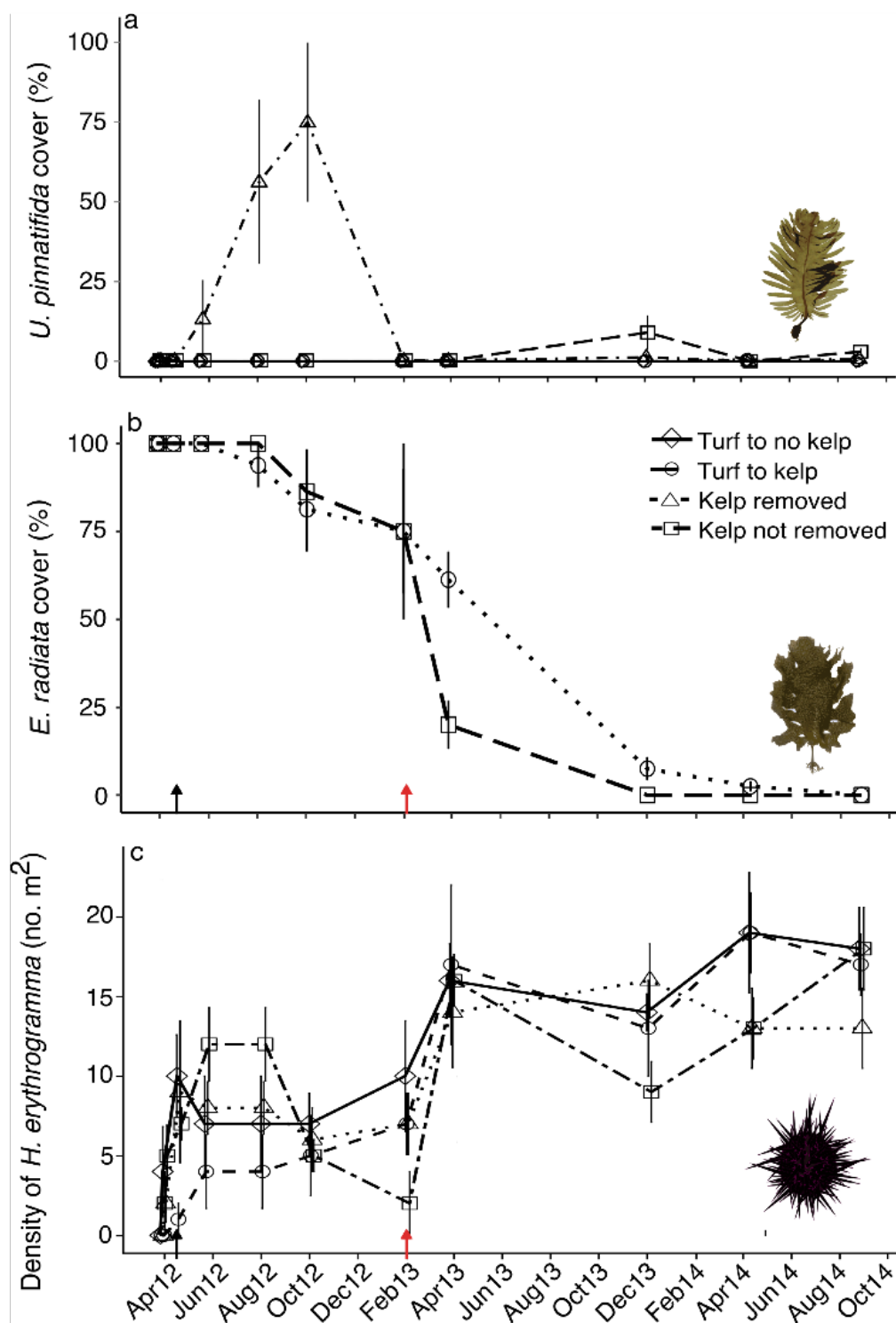


Figure 5 a) Percentage cover (mean \pm SE) of the invasive kelp *Undaria pinnatifida* under experimental treatments, combining treatments from Experiments 4 and 5. b) Percentage cover of *Ecklonia radiata* (mean \pm SE) contributing to the kelp treatments in Experiments 4 (i.e. 'Turf to kelp') and 5, (i.e. 'Kelp not removed'). c) Density of the sea urchin *Heliocidaris erythrogramma* on experimental rocks from long-term experiments 4 and 5, where treatments 'Turf to kelp' (n=4; circle and dash) and 'Turf to no kelp' (n=4; diamond and solid line) examined the effect of *E. radiata* presence and absence respectively; and 'Kelp cleared' (n=4; triangle and dotted line) and 'Kelp not removed' (n=4; square and dot-dash line) examined the effect of clearing *E. radiata*. These experiments ran for 840 days from March 2012 to October 2014. The black arrow indicates 30-day sampling for Expts. 1 and 2, red arrow indicates end of Expts. 1 and 2 and the start of the natural experiment.

Discussion

The balance among key interacting species, such as kelps, their competitors, and grazers contributes to the maintenance of kelp bed structure and functioning. The generality of the kelp-turf dynamic, the ‘turf clearance’ or ‘whiplash’ function of kelp sporophytes, and the contribution of this function to maintaining kelp beds is well established (Dayton 1975; Kennelly 1989; Connell 2003a; Strain et al. 2014). Here our results show clearly that sporophytes of either the native *E. radiata* or non-native *U. pinnatifida* can both remove and mitigate proliferation of turf, thus *U. pinnatifida* can act as a functional replacement of native kelp *E. radiata* in terms of the ‘turf clearance’ effect, but only for a limited time-frame due to its annual nature. This study extends the collective understanding of kelp-turf dynamics to include the effects of the invasive kelp *U. pinnatifida* and sea urchins. This is important as it is evident that urchins globally can be a key disturbing force to kelp beds (Ling et al. 2015; Krumhansl et al. 2016). The concerning implication of this study is that loss of kelps (both native and invasive) results in loss of primary production and energy flow between habitats. Replacement of kelps by persistent turfs represents a loss of structure and function, but future research is required to understand the capacity for turfs to provide primary and secondary production when kelps are not present.

The mechanism by which kelps clear the benthos has been well studied and is contributed in part by direct and indirect effects of the kelp thallus (Velimirov and Griffiths 1979; Kennelly 1987b; Kennelly 1989; Kiirikki 1996; Connell 2003a; Connell 2003b). Irving and Connell (2006) demonstrated the abrasive capacity of *E. radiata* on the benthos (estimated from rates of clearing of paint on painted tiles attached to the substratum). Additionally, Connell (2003) described strong negative effects of *E. radiata* lamina on a mosaic of articulated coralline and

filamentous turfing algae, with ~52% of the effect attributable to shading by the kelp, and 43-48% of the effect that was not accountable for by shading assumed to be due to abrasion by the kelp. It is likely that the clearance effect described for *E. radiata* and *U. pinnatifida* in the current study reflects the effects of physical scour (in the short-term), and the combined effects of scour and shading in the longer-term. For both kelps, the per capita effect of an individual thallus in clearing turf was linearly related to the length of the thallus. However, there was a difference between the effect of *U. pinnatifida* clearance (Exp. 1) and removal (Exp. 2) on turf. In PPB *U. pinnatifida* more often recruited onto microhabitats within the turf matrix, relative to *E. radiata* (Personal observation), resulting in *U. pinnatifida* covered rocks with high understory cover of turf. The initial high cover of turf meant that turf rapidly took up any available space following invasive kelp removal, in contrast to *E. radiata* where lower initial cover of turf resulted in more free space for turf to grow and cover over, in the 30 days, resulting in lower cover of turf following kelp removal. *U. pinnatifida* recruitment into microhabitats within turfs has also been observed in New Zealand (Schiel and Thompson 2012; Thompson and Schiel 2012; South et al. 2017). This shows that while both kelps can affect cover of turfs, the biological traits of different kelp species can influence the turf clearance function.

Given *U. pinnatifida*'s seasonal dieback, *U. pinnatifida* thalli only provide an equivalent or greater turf clearance function as the native kelp for 5 months of the year at best (see Fig 3b). Therefore, while *U. pinnatifida* can replace the clearance function for a period of time, it cannot entirely replace the role of the native *E. radiata* in maintaining reef free of turf. Nevertheless, turf clearance by *U. pinnatifida* is likely to be important in areas where the kelp canopy is already disturbed, such as on urchin barrens or turf 'meadows' at Williamstown. In

2474 these areas, the biological traits of *U. pinnatifida* (such as rapid growth, high reproductive
 2475 output, early and rapid maturation, and the ability to settle and develop to reproductive
 2476 maturity on almost any substratum) facilitate the ability to outpace the urchins capacity to
 2477 overgraze, or grow on loose substrata, and enables the alga to grow to reproductive maturity
 2478 in areas dominated by turfs and/or urchins (Valentine and Johnson 2003; Valentine and
 2479 Johnson 2005; South et al. 2017). However, once turf established, following grazing of *E.*
 2480 *radiata* and establishment and senescence of *U. pinnatifida*, recruitment of any kelp (native
 2481 or non-native) was reduced (i.e. lack of recruitment in the second year of the long terms
 2482 experiment). As such this lack of *U. pinnatifida* in the second year of the long-term
 2483 experiment, is likely due to turf competition as opposed to urchin grazing effects. Reduction
 2484 in *U. pinnatifida* abundance in the growing season following establishment of the invasive has
 2485 previously been established (Valentine and Johnson 2003; Schiel and Thompson 2012;
 2486 Thompson and Schiel 2012) and been linked to recovery of native species. During the present
 2487 study the native species to recover were turfs not native-canopy formers (as in Valentine and
 2488 Johnson, 2003). Die-back of *U. pinnatifida* occurs in the Austral spring at a similar timing to
 2489 recruitment of native kelps (Lilley and Schiel 2006). Therefore, the ‘turf-clearing’ effect of *U.*
 2490 *pinnatifida* and its seasonal die-back may provide microsites suitable for recruitment,
 2491 development and establishment – ‘safe sites’ (Harper et al. 1961) of native kelp aiding the re-
 2492 establishment of *E. radiata* beds i.e. kelp-patch formation theory: Velmirov and Griffiths
 2493 1979, however further work will be needed to test this and to further generalise the role of
 2494 turf clearance by *U. pinnatifida*.

2495

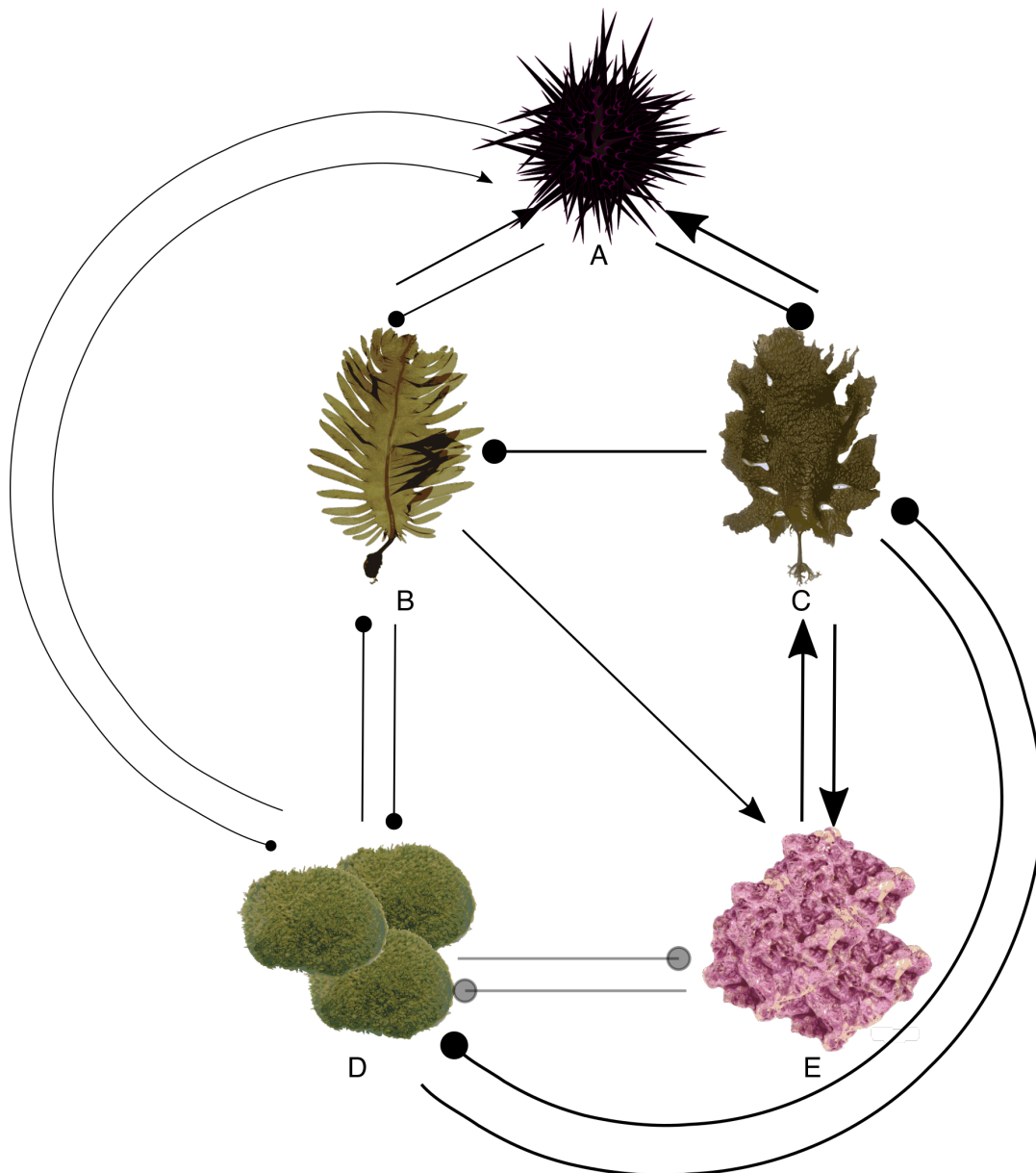
2496 There is a growing body of literature that suggests that *U. pinnatifida* can provide biogenic
 2497 habitat, biomass and significant inputs of carbon to invaded ecosystem (Dean and Hurd 2007;

2498 Suárez-Jiménez et al. 2015a; Suárez-Jiménez et al. 2015b; Tait et al. 2015; South et al. 2016;
 2499 Epstein and Smale 2017; Suárez-Jiménez et al. 2017). South et al. (2016) suggests that these
 2500 often-overlooked features of non-native species may well represent a net gain to invaded
 2501 communities and ecosystems. Given that it has generally proved to be costly and impractical
 2502 to eradicate *U. pinnatifida* (Forrest and Hopkins 2013; Epstein and Smale 2017), this may
 2503 represent more acceptable consequences of invasion than is usually associated with the
 2504 introduction of non-native species (South et al. 2017). Indeed, management efforts might be
 2505 better focussed on alternative threats or on proximate influences that encourage the spread
 2506 of *U. pinnatifida*, not on eradication of *U. pinnatifida* itself.

2507

2508 Over the duration of the current study, there was a steady increase in the influence of the
 2509 overgrazing sea urchin *Heliocidaris erythrogramma*, which was reflected as a reduction in the
 2510 cover of *E. radiata* in all experimental treatments and on the surrounding reef. The ongoing
 2511 decline of the native kelp reduced its clearance effect, resulting in an overall increase in turfs
 2512 (see Fig. 1h). The long duration of experiments 1 and 2 meant that two recruitment periods
 2513 for both kelp species occurred during the experiment, although limited kelp recruitment was
 2514 observed, consistent with inhibition of kelp recruitment by turfs (Kennelly 1987a; Reed 1990;
 2515 Worm and Chapman 1998). Thus, both kelp species have the capacity to mitigate
 2516 proliferation of turfs, but once kelp cover is lost turfs dominate space and can exclude kelps,
 2517 presumably by reducing 'safe sites' for recruitment (Fig. 6). Loss of kelps and shifts to turfs
 2518 influences the resilience of kelp beds as turfs can negatively affect the early-life history stages
 2519 of turfs (Filbee-Dexter and Wernberg 2018; O'Brien and Scheibling 2018). A shift from kelps
 2520 to turfs is likely to reduce the flows of kelp derived primary production within and between
 2521 ecosystems influencing secondary production, connectivity and marine food webs (Copertino

et al. 2005; Krumhansl and Scheibling 2011; Suárez-Jiménez et al. 2017; Filbee-Dexter et al. 2018). An assessment of the relative ecosystem function of kelps vs. turfs is necessary to truly assess the implication of shifts between these two groups and will lead to a more holistic understanding of the provision of services from ecosystems dominated by either kelps or turfs.



2527

Figure 6. Conceptual diagram summarising the interactions between sea urchins *Heliocidaris erythrogramma* (A), exotic kelp *Undaria pinnatifida* (B), native kelp *Ecklonia radiata* (C), turf (D), and encrusting coralline algae (E). Negative effects are filled circles; positive effects are an arrowhead, and no effect is indicated by no symbol. The thickness of connector lines and size of the symbol indicates the relative strength of the interaction. Solid black interactions indicate an interaction examined in

the study, while grey interactions indicate putative interactions previously established in the literature.

Conclusion

E. radiata strongly influences its local environment, which in turn alters understory structure, preventing or reducing the establishment of turfs. If these effects are reduced or eliminated by disturbance to native kelps (e.g. via sea urchin overgrazing), significant and persistent alterations in the algal community can occur (Fig. 6). On reefs in Port Phillip Bay, depending on the season in which they occur, gaps in kelp beds either become dominated by turf or *U. pinnatifida*. However, the *U. pinnatifida* is a winter annual and dies off during the period of peak recruitment of *E. radiata*. In contrast, turf persists year-around, and thus turf proliferation is more problematic as it has the capacity to reduce recruitment of *E. radiata* (e.g. Valentine and Johnson 2003, Kennelly 1987a, and Gorgula and Connell 2004). In areas where native kelp beds have been lost, any net recovery in ecological function derived from increased abundance of *U. pinnatifida* is limited by the annual nature of its sporophyte. Despite this, *U. pinnatifida* can provide the function of clearing turf algae, particularly in areas devoid of *E. radiata*. Nevertheless, the temperate reef ecosystem in this part of Port Phillip Bay appears to be shifting from kelp beds to a degraded and persistent turf-dominated state. Whether the turf-dominated state would persist at large scales in the absence of sea urchins is unknown. Irregardless, rocky reefs in this region appear to have transitioned into a novel regime characterised by extensive cover of turf, high abundance of urchins, with pulses of exotic kelp.

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2792 CHAPTER 4: Spatially-variable development
2793 of sediment-trapping turfs under elevated
2794 nutrients, sediment, and canopy disturbance
2795 correlates with canopy community
2796 composition

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Abstract

Globally, natural systems are threatened by multiple anthropogenic stressors. The single and interactive effects of these stressors can influence both the physical and biological interactions that define the resistance and resilience of a system. Here a multi-factorial field experiment at two sites is used to examine the resistance and resilience of kelp beds to multiple urban stressors (elevated nutrient and sediment regimes) in Port Phillip Bay (PPB), Australia's largest urbanised embayment. Significant variability between sites was observed in some responses to experimental manipulations, reflecting spatial variation in resistance and resilience of kelp bed communities. Differences in responses to treatments reflected that the canopy at one site was dominated by the laminarian kelp *Ecklonia radiata*, while at the other sites a diversity of furoid algae made up the canopy. At both sites, there was no evidence of any direct effects of elevated nutrients or sediments (at twice-ambient loads) on the cover of canopy-formers, while both added nutrients and canopy clearance acted additively to increase coverage of turfing algae. However, overgrowth of reefs by sediment-trapping turf algae reduced the recruitment of *E. radiata* but not of furoid canopy algae. Also, despite similar densities of sea urchins (*Heliocidaris erythrogramma*) at the two sites, the canopy of furoids showed strong resilience after removal and was not significantly consumed by the urchins, but there was no resilience of the laminarian kelp canopy, with very little change in canopy cover of laminarians through the experiment. At the site supporting intact *E. radiata*, sea urchins increased when nutrient was enriched, leading to canopy loss as a result of their overgrazing. The furoid-dominated seaweed beds suggest the potential emergence of a novel resistant and resilient assemblage under urban regimes. Whether the high resistance and resilience properties of the furoid canopy under an 'urbanised' environment reflects furoid biological characteristics (simple life-history with

2842 respect to laminarians, capacity to re-grow from vestigial remnants of holdfasts, recruit into
2843 turf-covered areas and poorly preferred by urchins), or is related to the species diversity of
2844 this canopy community, or both, is uncertain. Regardless, our findings indicate that seaweed
2845 bed resilience and resistance against turf-overgrowth may be more achievable by re-
2846 establishing a diverse canopy, including fucoids, than focussing on the recovery of the single
2847 laminarian kelp species (*Ecklonia radiata*) currently experiencing dramatic decline in PPB.
2848

Introduction

Human activities are exacerbating marine habitat loss at an ever-increasing rate (Hoekstra et al. 2005; Lotze et al. 2006; Worm et al. 2006). Centuries of overexploitation, habitat transformation, and pollution have precipitated ongoing loss of biodiversity and continued erosion of ecosystem stability (Adger et al. 2005; Lotze et al. 2006; Worm et al. 2006). When a system is stable it is thought to be both i) resistant (capacity to weather a disturbance without loss), and ii) resilient (capacity to recover from a disturbance after incurring loss) (Connell and Sousa 1983; Pimm 1984; Tilman and Downing 1996; Lake 2013; Nimmo et al. 2015). Resistance and resilience are often merged in the concept of ecosystem stability (Holling 1973; Folke et al. 2004). However, there is value in viewing them as closely related but separate concepts that are independently measurable (Lake 2013; Nimmo et al. 2015; Connell et al. 2016).

Loss of ecosystem stability is typically brought about by changes in the strength and types of ecological interactions, i.e. competition, predation, facilitation (Crain et al. 2008; Gunderson et al. 2016). In many instances, these changes are precipitated by the combined effects of multiple local (i.e. nutrient enrichment and over-harvesting) and global (warming and acidification) anthropogenic stressors. Multiple stressors often act at different scales (Crain et al. 2008) and can be further complicated by complex interactive (e.g. additive, synergistic, or antagonistic) effects (Gunderson et al. 2016) which can hamper identifying effective management strategies (Crain et al. 2008; Strain et al. 2014; Strain et al. 2015).

In some instances, non-additive interactions between multiple stressors have been linked to phase shifts to alternative stable states (Scheffer et al. 2001). Examples of

2874 alternative states can be found in many marine systems such as coral reefs (Mumby et al.
 2875 2006; Hughes et al. 2007; Fung et al. 2011) and kelp-based systems. In kelp beds, phase shift
 2876 to alternative states can be to dominance by sea urchins (Steneck et al. 2002; Konar and
 2877 Estes 2003; Ling et al. 2009; Steneck and Johnson 2014) or algal turf-sediment matrices
 2878 (Airoidi and Cinelli 1997; Gorgula and Connell 2004; Perkol-Finkel and Airoidi 2010). These
 2879 shifts all involve transitions from communities with high structural heterogeneity dominated
 2880 by kelps and other large habitat-forming seaweeds to communities low in structural
 2881 complexity, representing a simplification of habitat (Lawrence 1975; Airoidi et al. 2008;
 2882 Steneck and Johnson 2014; Ling et al. 2015).

2883

2884 The shift from complex luxuriant and biodiverse kelp beds to simplified habitats
 2885 dominated by turfing and ephemeral species is an emerging phenomenon worldwide (Strain
 2886 et al. 2014; Krumhansl et al. 2016, Filbee-Dexter and Wernberg, 2018, O'brien and
 2887 Schiebling, 2018). In the Mediterranean, this shift has been linked to elevated anthropogenic
 2888 sediment input (Airoidi and Virgilio 1998; Airoidi 2003; Balata et al. 2015). The morphology
 2889 and life-history characteristics of rapidly growing ephemeral and turf-forming taxa enables
 2890 binding and trapping of sediments into a consolidated algal-sediment matrix, which can
 2891 quickly colonise space freed by disturbance, e.g. by sediment burial and scour (Airoidi 2003;
 2892 Copertino et al. 2005; Perkol-Finkel and Airoidi 2010). In the Baltic (Eriksson 2002; Worm and
 2893 Lotze 2006) and some Australian metropolitan coastlines (Gorgula and Connell 2004; Gorman
 2894 and Connell 2009), anthropogenic nutrient loading also results in proliferation of turf-forming
 2895 algae so that normally subordinate taxa become dominant (i.e. *Ulva* spp. and *Pilayella*
 2896 *littoralis*), trapping sediment to form a semi-consolidated matrix (Connell 2014) and
 2897 displacing larger perennial macrophytes (Lotze et al. 2000; Gorman and Connell 2009;

2898 Gorman et al. 2009). In either situation, the newly established habitat is simplified and
2899 represents an impoverished community of reduced ecological diversity and functioning that
2900 can persist for decades, if not permanently, without management or restoration (Nyström et
2901 al. 2012; Campbell et al. 2014; Strain et al. 2014; Ling et al. 2015).

2902

2903 Here I examine the effect of multiple stressors (nutrients and sediments) on the stability of
2904 temperate reefs to inform approaches for restoration of declining kelp beds dominated by
2905 *Ecklonia radiata* (a laminarian) and a variety of fucoids. I utilised a multifactorial field
2906 experiment replicated at two sites in Australia's largest urbanised embayment, Port Phillip
2907 Bay in southern Australia (Fig. 1). I used cleared (i.e. complete removal of kelp beds) and
2908 intact kelp beds to understand the resistance-resilience properties of reef communities
2909 under multiple urban stressors. Examination of intact kelp bed canopies permitted
2910 investigation of system resistance, while experimental clearance of kelp bed canopies
2911 enabled examination of factors determining kelp recovery potential (resilience).

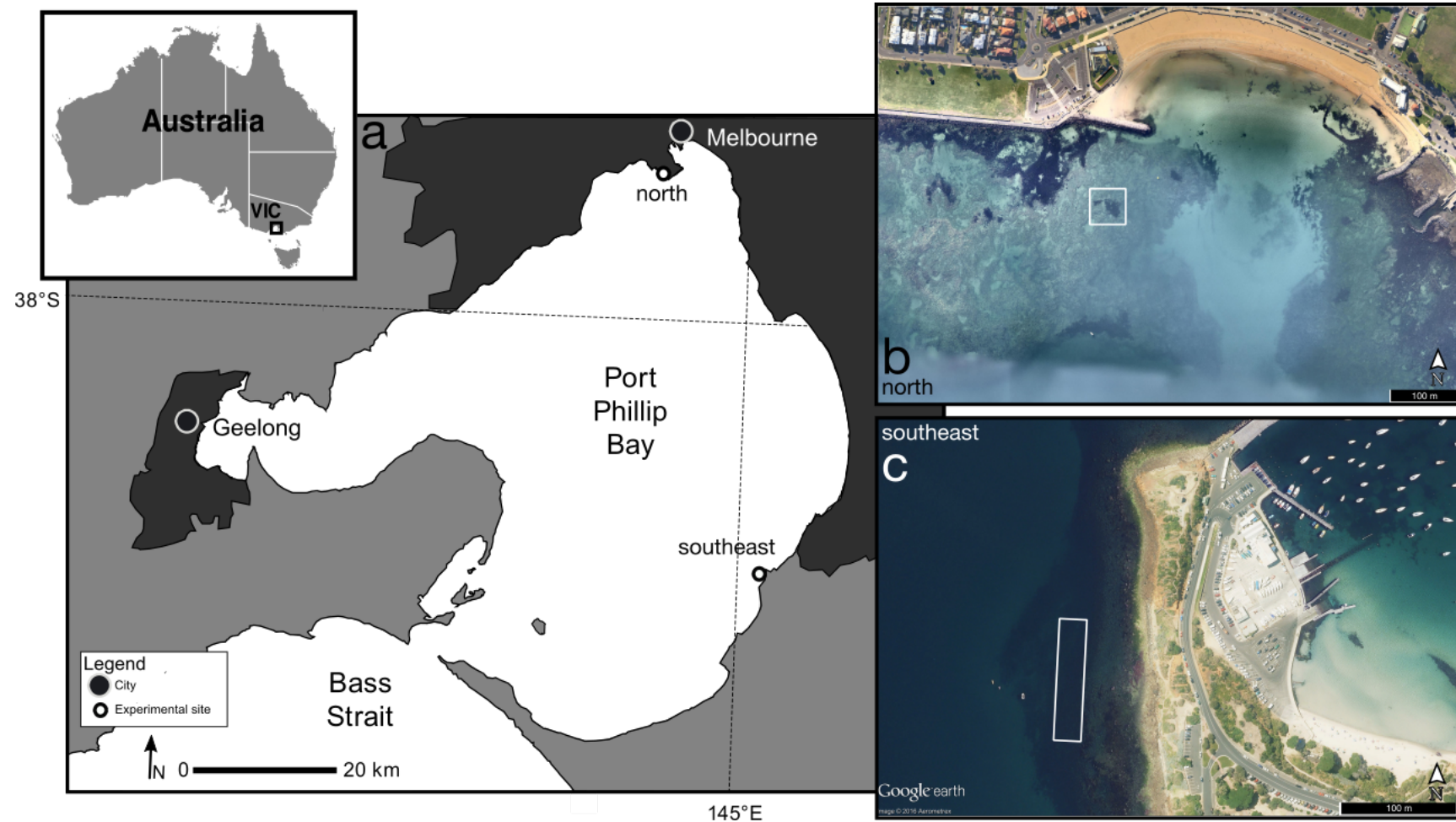


Figure 1. a) Map of Port Phillip Bay, an urbanised embayment in southeastern Australia, detailing the urbanised extent (dark grey polygon) of Melbourne and Geelong (large symbols, bounded in white) in relation to the experimental sites (small white symbols, bounded in black); b) shows the north study site, the dark remnant kelp beds (e.g. within white box) surrounded by lighter 'speckled' sea urchin barrens on reef devoid of macroalgae, grading to silty sand; c) shows the southeast study site. Experimental treatments were within the white bounding polygon

2918

2919 **Materials and Methods**

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2921 *Study sites and description*

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2923 Experimental sites were selected to represent kelp beds across northern and southeastern

2924 Port Phillip Bay (PPB), Australia's largest (1,930 km²) urbanised temperate embayment (Fig.

2925 1). The northern PPB site (S 37° 52' 10.5564", E 144° 53' 36.4884") is characterised by a

2926 shallow rocky reef composed predominantly of boulder and cobble interspersed by small (10

2927 m²) patches of sand. The reef extends from the intertidal to a depth of ~5 m where it grades

2928 into silty soft-sediment. The kelp bed (Fig. 1b: north) in the north was dominated by the

2929 canopy-forming laminarian *Ecklonia radiata* [(C. Agardh) J. Agardh 1848, Family:

2930 Lessoniaceae] with a simple understory community dominated by encrusting (non-

2931 geniculate) coralline algae (ECA). The introduced annual Japanese kelp *Undaria pinnatifida*

2932 [(Harvey) Suringar, 1873, Family: Alariaceae] also occurs in dense small stands forming a

2933 closed canopy covering ~0.5–1 m² (4-20 individuals per patch) on urchin barrens and in the

2934 ecotone between barrens and native kelp bed habitat. The kelp beds are interspersed by

2935 areas dominated by the sea urchin *Heliocidaris erythrogramma*, which forms and maintains

2936 sea urchin barrens with high cover of bare-rock and/or ECA, and mat-forming turf algae

2937 (Table S1 and S2). In the southeast (38°12'47.8836", E 145°1'56.517"), the reef follows the

2938 shoreline at a width of 40-100 m, the reef shelves from the intertidal down to the reef-edge

2939 where it grades to silty sand at ~6 m depth (Fig. 1c: southeast). The kelp bed in the southeast

2940 is composed of the canopy-forming *E. radiata* co-occurring with canopy-forming fucoid algae2941 (*Acrocarpia paniculata*, *Caulocystis uvifera* [(C. Agardh) Areschoug 1854, Family:2942 Sargassaceae], *Cystophora monilifera* and *C. moniliformis* [(Esper) Womersley & Nizamuddin2943 in Womersley 1964, Family: Sargassaceae], *Sargassum vestitum* [(R.Brown ex Turner)

2944 C.Agardh 1820, Family: Sargassaceae], *S. decipiens* and *S. fallax* [Sonder 1845, Family:
 2945 Sargassaceae]], and a much more diverse understory community than in the north (Appendix
 2946 1 and 2). The invasive *U. pinnatifida* does not occur at this site. All experimental plots at both
 2947 sites were established at 3-4 m depth. PERMANOVA and SIMPER analysis of initial algal and
 2948 faunal communities showed that before applying treatments, treatment groups differed only
 2949 between sites (Appendix 2, 5 and 6). Thus, any differences among treatment groups within
 2950 sites at the conclusion of the experiment were attributable to treatment effects.

2951

2952 *Experimental design and data collection*

2953

2954 The experiment consisted of 3 crossed factors: canopy removal (2 levels, +/- canopy), nutrients
 2955 (2 levels, enhanced/ambient), sediment (2 levels, enhanced/ambient). Treatments were
 2956 applied to 3 replicate 1.5 m * 1.5 m plots within intact kelp beds at the two sites, amounting
 2957 to 4 main effects in total (all fixed) and 48 experimental plots (24 plots at each site). Each plot
 2958 had a central star-picket and another in one corner to define a spatially fixed 1 x 1 m area
 2959 within the centre of each plot. All experimental plots were >5 m away from any other plot to
 2960 ensure no interaction of treatments between plots (this distance was shown to be sufficient
 2961 by Worm et al. (2000) and Russell and Connell (2005a) when adding nutrients to experimental
 2962 plots as performed here).

2963

2964 *Disturbance*

2965

2966 Treatments of entire removal of canopy-forming algae were undertaken using a paint scraper
 2967 to remove all thalli inclusive of the holdfast. All canopy-forming species (Laminariales (*E.*
 2968 *radiata* and *Undaria pinnatifida* and fucoids (*A. paniculata*, *C. uvifera*, *C. monilifera* and *C.*
 2969 *moniliformis*, *S. vestitum*, *S. decipiens* and *S. fallax*) were removed from the 1.5 x 1.5 m algal

2970 canopy 'Clearance' plots. The 0.25 m clearance buffer around the 1 m² area that was
 2971 censused ensured no physical influence of the surrounding canopy forming species on the
 2972 cleared plots.

2973

2974 *Nutrient enrichment*

2975

2976 Mesh bags (100 x 100 mm with 1 mm aperture mesh) containing 200 g of Osmocote® Pro (3-
 2977 4 M, 17N:4.8P:8.3K) slow release fertiliser were attached to the central star picket in
 2978 designated plots. Ambient nutrient plots received a bag with small pebbles as a procedural
 2979 control. To ensure a constant supply of nutrients, the bags were replaced every six weeks.

2980 The technique and calculation of the amount of fertilizer used were according to Worm et al.
 2981 (2000) and based on observations by Connell and colleagues in South Australia who showed
 2982 that this approach realised increases of 88%, 58%, ~39% and ~38% for ammonia, nitrate,
 2983 nitrite and phosphorus, respectively, following addition of 3g Osmocote (Gorgula and Connell
 2984 2004), and 84% elevation in nitrate levels with 12 g of Osmocote (Russell and Connell 2005b).

2985 Water samples to quantify local nutrient elevation in treatment plots were taken midway
 2986 through one treatment period (three weeks after exchange of nutrient-filled mesh bags). 50
 2987 ml samples were taken with a 60 ml syringe held 200 mm away from the nutrient bags,
 2988 filtered into 60 ml falcon tubes and kept on ice for <2 hours until they could be frozen.

2989 Samples were tested for concentrations of nitrite, nitrate, ammonia (NH₃), and filterable
 2990 reactive phosphorus (FRP) at the Water Studies Centre, School of Chemistry, Monash
 2991 University, Victoria. Results were analysed with a two-way PERMANOVA, where treatment (2
 2992 levels: ambient with six replicates and enhanced with six replicates) and site (2 levels: north
 2993 and southeast) were treated as fixed and orthogonal. Euclidean distance dissimilarity
 2994 matrices were computed with 9999 permutations. The analysis showed a significantly

2995 elevated dissolved nutrient concentration on plots with fertiliser (Two-way PERMANOVA,
 2996 nutrient effect: Pseudo- $F_{1,20} = 5.40$, $P_{(\text{permutational})} = 0.02$) with non-significant differences
 2997 between sites and an insignificant interaction (Appendix 3). Measurement of ambient
 2998 nutrient concentrations shows that nutrient concentrations are broadly similar at both sites
 2999 (Appendix 5c). I achieved significant elevations in dissolved nutrient concentrations for the
 3000 treatment plots (Appendix 5d).
 3001
 3002 *Sediment enhancement*
 3003
 3004 Sediment enhancement involved doubling the ambient sediment load received by each reef
 3005 every six weeks (Appendix 5). This level of sediment addition was performed in pilot trials and
 3006 deemed to be ecologically meaningful while not wholly smothering smaller algae and
 3007 invertebrates. Ambient sediment loading was determined from sediment flux rates estimated
 3008 using sediment traps ($n = 3$ replicate baffled cylindrical PVC sediment traps, 600 mm height *
 3009 100 mm diameter, stationed 50-100 m apart in kelp and urchin barren habitats at both sites
 3010 for ~12 months before the start of the manipulative experiment). Sediment traps were
 3011 deployed and retrieved by SCUBA every six to eight weeks. Sediments were settled,
 3012 supernatant water removed, and dried in aluminium trays (160*80*225 mm) to constant
 3013 weight at 60°C. The dry weight of the sample was utilised to calculate total sediment
 3014 depositional load ($\text{g m}^{-2} \text{d}^{-1}$). Sediment load was more variable in the southeast than in the
 3015 north, resulting in different treatment loads between the sites (Appendix 5a and b).
 3016 Sediments added to the experimental plots were collected by SCUBA diver, using a screw-top
 3017 barrel and scoop, from nearby sediment-dominated locations that had a similar particle size
 3018 distribution as occurred naturally on the reef. The collected sediments were placed into a
 3019 header tank on board the research vessel, then added to plots as a “sediment rain” (Airolidi

and Virgilio 1998) by a SCUBA diver operating a flexible 25 mm diameter plastic hose from the header tank. However, exact matching of the size-distribution of ambient deposited sediments was difficult, and our sediment treatments had higher proportions of the sand size fraction than was collected in sediment traps (Appendix 5b). This likely reflected that some portion of the fine sediments represented in the sediment traps were further mobilised in the natural reef habitat and settled elsewhere.

An initial survey was made of both the macroalgae and faunal community undertaken before application of any treatments, and this assessment repeated every three months over the 16-month duration of the experiment. The percentage cover of all algae and counts (density) of the important laminarian *Ecklonia radiata* (as per Kirkman 1981), *U. pinnatifida* (defined as: Stage I individuals that are teardrop to oblong in shape with no pinnae or midrib, Stage II individuals have a midrib and developed or developing pinnae, but no sporophyll, Stage III individuals are fully developed with pinnae and sporophyll) and fucoid species at different stages of development (Juveniles: defined as thalli with low lying basal leaves and no evidence of axes, floats or receptacles; Adults: evidence of axes even if regressed and receptacles and floats when reproductive) were made within a 1 x 1 m quadrat. I also quantified percentage cover and depth of the turf-sediment matrix (hereafter referred to as turf). For turf depth, five replicate measurements were taken using a metal ruler (one measurement was taken in each of the 0.25 m² quadrants of the full assessment quadrat, plus one additional random point). I assessed the density of sessile and mobile invertebrates in each plot including the urchin *H. erythrogramma*, which is known to overgraze and create extensive sea urchin barren in PPB (Constable 1990; Carnell and Keough 2016; Kriegisch et al. 2016). Urchin density was converted to biomass using local allometric relationships (after

3044 Kriegisch 2016). Urchin biomass was calculated by using the allometric relationship between
 3045 test diameter and fresh weight determined for each site (determined from $n = 60 - 90$
 3046 urchins per site). Urchin density was converted to biomass density from the test diameter of
 3047 $n = 10$ randomly collected urchins. Note that because of the non-linear relationship, the
 3048 allometric equation was used on each urchin individually to estimate individual biomass, and
 3049 then the average of these biomasses was utilised.

3050

3051 *Estimating reproductive output of Ecklonia radiata*

3052

3053 At the final assessment, I also measured reproductive output of *E. radiata* in all uncleared
 3054 plots by destructively sampling two fully developed sporophytes (i.e. Stage III sporophyte
 3055 according to the classification scheme of Kirkman (1981)) from each plot (thus $n = 6$ *E.*
 3056 *radiata* per treatment per site). Propagule pressure for *E. radiata* was calculated as the
 3057 propagules per square metre of reef based on the method of Mohring et al. (2013). Because
 3058 most of the sorus-tissue was located on the midrib, laterals were first trimmed away from the
 3059 mid-rib, the mid-ribs were then desiccated (1-hour air drying at room temperature), the
 3060 percentage of the mid-rib covered by sori determined (using point estimates with a grid of
 3061 points at 10 mm spacing), and individual sori subsampled by punching consecutive discs of
 3062 sorus tissue (27 mm diameter) in a line from the distal end to the base of the mid-rib. These
 3063 discs were then soaked together in 50.0 ml of filtered seawater for 20 minutes. After soaking
 3064 0.1 mL of 70 % ethanol was added. The number of zoospores in two 1*1 mm (0.1 μ L) grids
 3065 was counted using a Neubauer counting chamber loaded with 1 ml of zoospore solution for a
 3066 total of three subsamples (six 1*1 mm grids). The results were averaged and expressed as the
 3067 number of zoospores released per unit area of sori sampled (i.e. total area of discs of tissue).
 3068 I calculated the zoospores produced per sporophyte by multiplying the number of zoospores

released by the area of sorus tissue. Propagule pressure was estimated as the mean zoospore production per sporophyte multiplied by mean sporophyte density.

Data analysis

Before all parametric analyses, data were checked for conformity to assumptions of homoscedasticity and normality. Where data were heteroscedastic, the transformation to stabilise variances was determined by the Box-Cox procedure within the MASS package in R (Venables and Ripley 2002). Where appropriate, multiple range tests were conducted using Tukey's honest significant difference test. All analyses were undertaken using the R package version 3.1.2 (R Development Core Team 2015) running in RStudio version 1.0.136 (RStudio Team 2015). All variables apart from recruits were analysed based on measurements made at the final sampling. Recruits for total canopy, *E. radiata*, and fucoids were analysed at the peak of recruitment for each.

Multivariate analyses of algal and faunal assemblage composition included PERMANOVA, CAP, and SIMPER (Clarke et al. 2014) Bray-Curtis resemblance matrices using PRIMER 7 and the PERMANOVA+ add-on (Clarke and Gorley 2015). On occasion, it was necessary to transform data before calculating Bray-Curtis matrices, details of transformations are given in the Results section. Community composition was contrasted among sites (north versus southeast), canopy clearance (uncleared (C-) versus cleared (C+)), nutrient enrichment (ambient (N-) versus enriched (N+)) and sediment elevation (ambient (Se-) versus doubling ambient (S+)) treatments. All factors were fixed and orthogonal. Bray-Curtis dissimilarity matrices were computed with 9999 permutations. Vector plots were produced in association with CAP ordinations to identify taxa most correlated with CAP axes

(based on Spearman correlations with a threshold $R > 0.5$). SIMPER analysis was used to identify taxa largely accounting for observed differences in assemblage composition within and between sites. For all ANOVA and PERMANOVA analyses, effect sizes were calculated using the partial omega squared index (ω_p^2) of Olejnik and Algina (2003):

$$\omega_p^2 = \frac{(\text{df_Error} \times (\text{MS}_{\text{Effect}} - \text{MS}_{\text{Error}}))}{(\text{SS}_{\text{Effect}} + (\text{n}_{\text{Total}} - \text{df}_{\text{Effects}}) \times \text{MS}_{\text{Error}})}$$

Results

Canopy-formers

Interestingly, there was a contrasting response to elevated nutrients on canopy-former cover between sites. All nutrient elevated treatments (N:◆, Se:✚, C&N:◇ and C&N&Se:○) in the north showed significantly reduced cover, while for the southeast site elevated nutrient treatments resulted in increased cover (Fig. 2a, Table 1, 2a and 3). In the cleared plots at both sites, over 16 months, canopy cover did not recover to that of adjacent uncleared plots, resulting in a significant effect of Clearance (Table 1 and Table 3) in both ANOVA and PERMANOVA (Table 2).

By decomposing the canopy-formers into the two major guilds, i.e. Laminariales (*Ecklonia radiata*: Fig. 3b and e) and fucoids (*Acrocarpia paniculata*, *Caulocystis uvifera*, *Cystophora monilifera* and *C. moniliformis*, *Sargassum vestitum*, *S. decipiens* and *S. fallax*) (Fig. 3c and f), I examined the contribution of each guild to maintaining canopy-former cover. In the southeast, the increases in canopy (Figs. 2a and 3a) were solely driven by increases in density of fucoids (Fig. 3a and c), not *E. radiata* as there was a continued decline in *E. radiata* abundance throughout the experimental period (Fig. 3b), and in contrast to the fucoids,

3116 there was no resilience (Table 1 and 3, Fig. 3). There was a peak in furoid recruitment
3117 observed in winter (May 2013) in the southeast (Fig. 3c and f). The ANOVA based on
3118 observations at the end of the experimental period identifies that the Clearance treatment
3119 did not significantly affect furoid cover or density (Table 1 and 3) showing that furoids
3120 strongly recruited into cleared plots so that by the end of the experiment density of furoids
3121 was similar in cleared and uncleared plots (Fig. 3f and Table 1 and 3).

Table 1. Results of a four-factor model I ANOVA examining the influence of site (north (Nth) *versus* southeast (SE)), canopy clearance (uncleared (C+) *versus* cleared(C-)), nutrient enrichment (ambient (N-) *versus* enriched (N+)), and sediment elevation (ambient (Se-) *versus* elevated (Se+)) on key characteristics of the kelp bed community at the conclusion of the experiment. Significant terms are in bold and underlined, with results of pair-wise tests for significant terms given in the lower section of the table.

		Canopy-former cover		Canopy-former recruits		Understory cover		EASM cover		EAC cover		<i>E. radiata</i> cover		<i>E. radiata</i> total		<i>E. radiata</i> recruits		<i>E. radiata</i> Propagule Pressure		Fucoid cover		Fucoid total		Fucoid recruits		<i>H. erythrogramma</i> biomass			
		sqrt(Y)		(Y)		log(Y+0.1)		(Y+0.1)^0.7		log(Y+1.0)		(Y+0.1)^0.2		(Y+0.1)^0.4		(Y+0.1)^0.2		log(Y+15)		(Y+0.1)^0.3		sqrt(Y+1)		sqrt(Y)		(Y+0.1)^0.85			
Source	df	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	df	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	
Site (S)	1	3.68.	0.05	3.39	0.05	<u>93.189***</u>	<u>0.66</u>	4.112.	0.06	<u>96.30***</u>	<u>0.66</u>	<u>7.75**</u>	<u>0.12</u>	<u>9.25**</u>	<u>0.15</u>	<u>15.07***</u>	<u>0.23</u>	1	0.99	0.04	<u>148.89***</u>	<u>0.75</u>	<u>55.44***</u>	<u>0.53</u>	0.96	0.00	<u>5.69*</u>	<u>0.09</u>	
Clearance (C)	1	<u>32.07***</u>	<u>0.39</u>	2.06	0.02	0.001	0.02	<u>18.84***</u>	<u>0.27</u>	<u>27.54***</u>	<u>0.36</u>	<u>59.01***</u>	<u>0.55</u>	<u>38.72***</u>	<u>0.44</u>	1.82	0.02	-	-	-	2.67	0.03	0.11	0.02	1.27	0.01	3.48.	0.05	
Nutrient (N)	1	<u>5.318*</u>	<u>0.08</u>	0.80	0.00	<u>13.67***</u>	<u>0.21</u>	<u>5.29*</u>	<u>0.08</u>	1.38	0.01	3.09.	0.04	<u>4.29*</u>	<u>0.06</u>	1.23	0.01	1	0.82	0.02	<u>11.74**</u>	<u>0.18</u>	<u>5.57*</u>	<u>0.09</u>	0.91	0.00	0.02	0.02	
Sediment (Se)	1	0.07	0.02	0.08	0.02	1.587	0.01	0.01	0.02	0.02	0.02	0.20	0.02	0.02	0.02	0.64	0.01	1	0.12	0.03	0.31	0.01	0.16	0.02	0.34	0.01	0.11	0.02	
S x C	1	1.48	0.009	1.50	0.01	1.22	0.01	<u>4.61*</u>	<u>0.07</u>	3.78.	0.05	0.06	0.02	0.11	0.02	<u>15.33***</u>	<u>0.23</u>	-	-	-	<u>15.20**</u>	<u>0.23</u>	<u>4.47*</u>	<u>0.08</u>	<u>12.01**</u>	<u>0.19</u>	1.72	0.01	
S x N	1	<u>16.00***</u>	<u>0.24</u>	0.18	0.02	<u>13.48***</u>	<u>0.21</u>	<u>4.82*</u>	<u>0.07</u>	0.70	0.01	<u>4.77*</u>	<u>0.07</u>	<u>5.24*</u>	<u>0.08</u>	0.01	0.02	1	0.52	0.00	<u>22.20**</u>	<u>0.31</u>	<u>10.75**</u>	<u>0.17</u>	0.13	0.02	<u>4.44*</u>	<u>0.07</u>	
C x N	1	0.09	0.02	0.32	0.01	1	0.00	0.41	0.01	0.29	0.02	0.02	0.02	0.48	0.01	0.52	0.01	-	-	-	4.04	0.06	1.87	0.02	1.04	0.02	0.00	0.02	
S x Se	1	0.14	0.02	2.37	0.03	1.97	0.02	0.02	0.02	2.01	0.02	0.00	0.02	0.02	0.02	0.42	0.01	1	1.11	0.04	0.01	0.02	0.01	0.02	0.00	0.01	0.22	0.02	
C x Se	1	0.07	0.02	1.34	0.01	0.51	0.01	1.24	0.00	1.18	0.00	0.12	0.02	0.63	0.01	1.06	0.00	-	-	-	0.03	0.02	0.56	0.01	0.10	0.04	0.77	0.00	
N x Se	1	0.21	0.016	0.72	0.01	0.79	0.00	0.16	0.02	0.38	0.01	0.47	0.01	1.01	0.00	0.84	0.00	1	0.25	0.02	0.90	0.00	0.52	0.01	0.74	0.00	0.44	0.11	
S x C x N	1	2.56	0.031	2.04	0.02	0.91	0.00	<u>5.24*</u>	<u>0.08</u>	1.22	0.01	3.69.	0.05	2.00	0.02	0.63	0.01	-	-	-	0.33	0.01	0.97	0.00	3.15.	0.02	0.08	0.02	
S x C x Se	1	0.01	0.021	1.37	0.01	0	0.02	0	0.02	1.90	0.02	0.05	0.02	0.00	0.02	0.42	0.01	-	-	-	0.31	0.01	0.51	0.01	0.84	0.00	0.85	0.00	
S x N x Se	1	0.00	0.021	0.05	0.02	1.74	0.02	0.08	0.02	0.00	0.02	0.13	0.02	0.05	0.02	0.08	0.02	1	0.03	0.04	1.79	0.02	0.05	0.02	0.01	0.02	0.67	0.01	
C x N x Se	1	0.04	0.02	0.56	0.01	1.21	0.00	0.65	0.01	0.14	0.02	0.01	0.02	0.24	0.02	0.00	0.02	-	-	-	0.01	0.02	0.06	0.02	0.72	0.01	1.23	0.01	
S x C x N x Se	1	0.02	0.021	0.06	0.02	0	0.02	0.12	0.02	0.01	0.02	0.39	0.01	0.25	0.02	0.70	0.01	-	-	-	1.89	0.02	0.34	0.01	0.06	0.02	2.54	0.03	
Error	32																		16										
Pair-wise tests																													
S						SE>Nth				Nth>SE		Nth>SE		Nth>SE		Nth>SE				SE>Nth		SE>Nth				SE>Nth			
C		C->C+								C->C+		C->C-		C->C-															
N																													
S x N		SE:N+&NthN->NthN+				SE:N+>NthN->NthN+		Nth:N+>Nth:N-&SE:N+>Nth:N-												SE:N+&N->Nth:N->Nth:N+		>Nth:N->Nth:N+							
S x C								Nth:C+>Nth:C-&SE:C+>Nth:C-						Nth:C->Nth:C+&SE:C+>Nth:C-						SE:C+&C->Nth:C+>Nth:C-		SE:C+&C->Nth:C+&C-		Nth:C+&SE:C+>Nth:C-		SE:N->Nth:N-			
C x N										Nth:N->Nth:N+&SE:N+>Nth:N+&SE:N+																			
S x C x N								Nth:C+>Nth:C-&SE:C+>Nth:C-&SE:C->Nth:C+>Nth:C-																					

3126

Notes: Variables are canopy-former cover, total canopy-former recruited sporelings, understory cover, epilithic-algal-sediment-matrix (EASM) cover, encrusting coralline algae (ECA) cover; cover, total sporophytes, number of newly recruited sporelings, and propagule pressure of the Australian kelp *Ecklonia radiata*; cover, total sporophytes, and counts of newly recruited fucoid sporelings and biomass of the sea-urchin *Heliocidaris erythrogramma*. Transformations required to stabilise variances and maintain heteroscedasticity are detailed beneath the respective variable, degrees of freedom and F-values with indicators of significance shown alongside the partialled effect size for

3131 each term as partial omega squared (ω^2). For significant terms from the ANOVA model, the respective pair-wise analysis is detailed below with significant groups separated
3132 by > and non-significant groups by =. Significance codes: $p > 0.05 < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

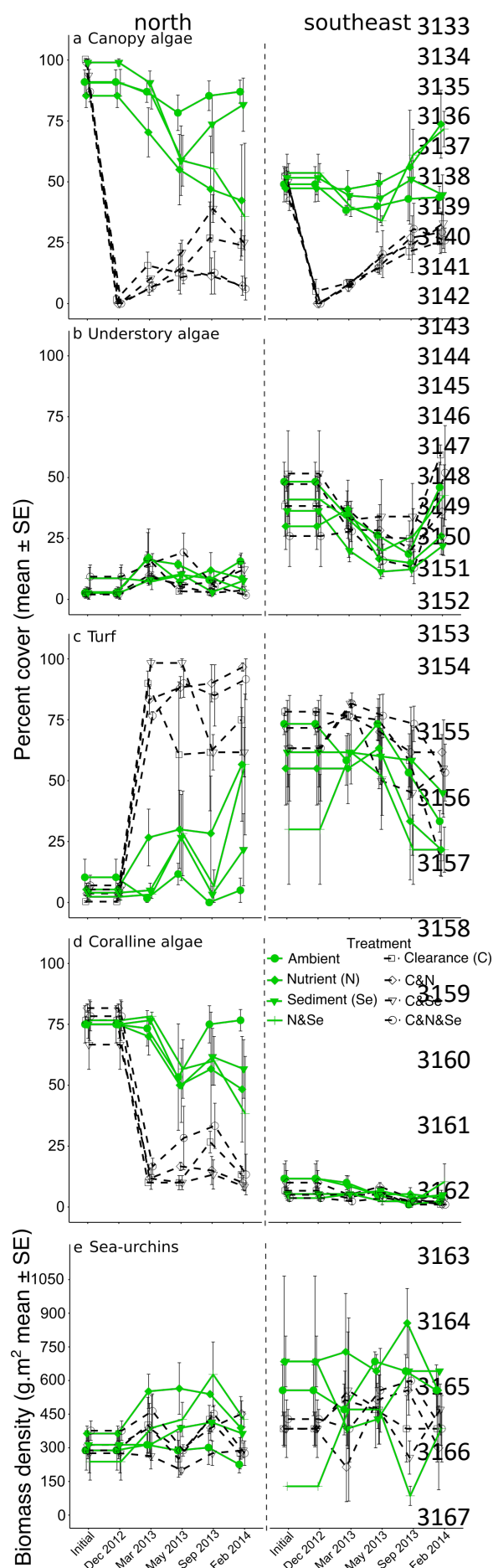


Table 2a Results of PERMANOVAs examining the influence of site (north *versus* southeast), canopy clearance (uncleared (C-) *versus* cleared (C+)), nutrient enrichment (ambient (N-) *versus* enriched (N+)), and sediment elevation (ambient (Se-) *versus* elevated (S+)) on algal and faunal communities. df = degrees of freedom, P(perm) = permuted P-values, ω_p^2 = partial effect size for each term as partial omega squared, significant terms are in bold and underlined.

a)	Algal community				Faunal community		
Source	df	Pseudo-F	P(perm)	ω_p^2	Pseudo-F	P(perm)	ω_p^2
Site (S)	1	<u>90.15</u>	<u>0.00</u>	<u>0.65</u>	<u>18.91</u>	<u>0.00</u>	<u>0.28</u>
Clearance (C)	1	<u>14.15</u>	<u>0.00</u>	<u>0.22</u>	1.26	0.28	0.01
Nutrients (N)	1	<u>2.77</u>	<u>0.03</u>	<u>0.04</u>	<u>2.36</u>	<u>0.03</u>	<u>0.03</u>
Sediment (Se)	1	2.04	0.08	0.02	1.34	0.24	0.01
S x C	1	<u>3.96</u>	<u>0.01</u>	<u>0.06</u>	0.80	0.57	0.00
S x N	1	<u>4.86</u>	<u>0.00</u>	<u>0.08</u>	1.11	0.37	0.00
S x Se	1	1.03	0.41	0.00	1.64	0.15	0.01
C x N	1	0.24	0.91	0	1.12	0.36	0.00
C x Se	1	0.19	0.93	0	0.56	0.77	0.00
N x Se	1	0.09	0.96	0	0.33	0.90	0.00
S x C x N	1	<u>2.40</u>	<u>0.05</u>	<u>0.03</u>	1.33	0.25	0.01
S x C x Se	1	0.63	0.67	0	1.03	0.42	0.00
S x N x Se	1	0.48	0.78	0	0.32	0.90	0.00
C x N x Se	1	0.27	0.90	0	0.56	0.76	0.00
S x D x N x Se	1	0.29	0.89	0	0.57	0.76	0.00
Residual	32						
Total	47						

Table 2b Pair-wise similarity matrix between/within pairs of the term Site x Clearance x nutrient for the algal community at the conclusion of the experiment. Significant terms are in bold and underlined.

	north(C- N-)	north(C+N- N+)	north(C- N+)	north(C+N+)	southeast(C- N-)	southeast(C+N- N+)	southeast(C- N+)	southeast(C+N+)
north(N-C-)	<u>80.57</u>							
<u>north(C+N-)</u>	<u>59.66</u>	<u>76.61</u>						
<u>north(C-N+)</u>	<u>66.63</u>	66.49	<u>67.58</u>					
north(C+N+)	<u>52.94</u>	<u>72.39</u>	70.94	<u>82.38</u>				
<u>southeast(C-N-)</u>	<u>35.13</u>	<u>46.35</u>	<u>38.36</u>	<u>42.41</u>	<u>73.10</u>			
<u>southeast(C+N-)</u>	<u>28.38</u>	<u>40.46</u>	<u>32.31</u>	<u>38.59</u>	<u>70.68</u>	<u>73.73</u>		
southeast(C-N+)	<u>34.70</u>	<u>39.65</u>	<u>33.72</u>	<u>34.91</u>	70.83	<u>62.74</u>	<u>68.88</u>	
<u>southeast(C+N+)</u>	<u>27.46</u>	<u>41.98</u>	<u>32.91</u>	<u>40.24</u>	<u>69.81</u>	74.88	<u>64.17</u>	<u>73.62</u>

Table 3. Summary of ANOVA results examining the influence of site (north versus southeast), canopy-former clearance (C: uncleared *versus* cleared), nutrient enrichment (N: ambient *versus* enriched), sediment elevation (Se: ambient *versus* elevated) on key characteristics of the kelp bed community at the conclusion of the experiment. The symbols (-) indicates a significant negative response; (+) indicates significant positive response (significant effects are grey-shaded) and (●) indicates non-significance.

Variable	Site (S)	Clearance (C)	Nutrient (N)	Sediment (Se)	CN	CSe	NSe	CNSe
Canopy-former cover	north	-	-	●	●	●	●	●
	southeast	-	+	●	●	●	●	●
recruits	north	●	●	●	●	●	●	●
	southeast	●	●	●	●	●	●	●
Understory	north	●	-	●	●	●	●	●
	southeast	●	●	●	●	●	●	●
Turf-sediment matrix cover	north	+	+	●	+	●	●	●
	southeast	●	●	●	●	●	●	●
Encrusting coralline algae	north	-	●	●	●	●	●	●
	southeast	-	●	●	●	●	●	●
Ecklonia radiata cover & counts	north	-	●	●	-	●	●	●
	southeast	-	●	●	●	●	●	●
recruits	north	-	●	●	●	●	●	●
	southeast	●	●	●	●	●	●	●
propagule pressure	north	●	●	●	●	●	●	●
	southeast	●	●	●	●	●	●	●
fucoids cover & counts	north	+	-	●	●	●	●	●
	southeast	●	●	●	●	●	●	●
recruits	north	+	●	●	●	●	●	●
	southeast	●	●	●	●	●	●	●
Heliocidaris erythrogramma biomass	north	●	●	●	●	●	●	●
	southeast	●	●	●	●	●	●	●
Total richness	north	●	-	●	●	●	●	●
	southeast	●	-	●	●	●	●	●
Canopy-former richness	north	●	-	●	●	●	●	●
	southeast	-	-	●	●	●	●	●
Understory richness	north	●	●	-	●	●	●	●
	southeast	●	●	+	●	●	●	●
Faunal richness	north	●	-	●	●	●	●	●
	southeast	●	-	●	●	●	●	●

In the north, elevated nutrients resulted in lower density of furoids compared to plots subject to ambient nutrient levels (Table 1 and 3). The only significant recovery in density of canopy formers, in the north, was due to recruitment of furoids (not *E. radiata*) into cleared plots not enriched with nutrients (C:□ and C&Se:▽; Fig. 3c and b, Table 1 and 3). Two strong peaks in density of canopy formers were observed in March and May 2013, in the north (Fig. 3a and d). The peak in March was driven by strong recruitment of furoid recruits. In May (winter) this signal was not due to *E. radiata* (Fig. 3b and e) or furoids (Fig. 3c and f), but occurred due to recruitment of the invasive *Undaria pinnatifida*. Similar to the effects on total canopy-former cover and furoid density, elevated nutrients also had a significant negative effect on *E. radiata* density in the north. In all instances, our experimental elevation of sedimentation had little discernible effect on canopy-forming species.

Understory

There was greater understory cover and richness in the southeast than in the north (Fig. 2b and appendix 6c), and nutrient enrichment in the north had a similar negative effect on understory, with the nutrient treatment resulting in lower understory cover compared to plots with ambient nutrients. Like our observations of canopy-formers, experimental doubling of sediment loads had no detectable effect on univariate measures of understory taxa (Table 1 and 3, Fig. 2).

Turf

Turf cover was initially higher in the southeast than in the north, however, when the canopy was cleared turf cover increased rapidly in the north (Fig. 2c). Additionally, increases in turf cover were also observed on uncleared plots once the canopy began to decline, in the north

(N:◆, Se:✚; Fig. 2c and a). Canopy clearance and nutrient enrichment resulted in an additive positive effect on the cover of turf relative to the separate effects of clearance and nutrient enrichment treatments (Table 1 and 3). Surprisingly, doubling of sediment loads did not significantly affected turf cover (Table 1 and 3, Fig. 2).

Encrusting coralline algae

Encrusting coralline algae (ECA) showed very similar patterns to that of *E. radiata* cover (Fig. 3d and Fig. 4b). Higher cover of *E. radiata* at the northern site correlated with higher coverage of ECA, while at the southeastern site cover of both *E. radiata* and ECA was low (Fig. 3d). Similarly, at both sites, there was a distinct drop in ECA cover following canopy removal, which showed no sign of increased cover over the duration of the study (Table 1 and 3, Fig. 2d).

Sea urchins

There was higher variability in biomass density of the sea urchin *Heliocidaris erythrogramma* in the southeast compared to the north, although mean biomass density across the two sites was similar. While the ANOVA shows little evidence of treatment effects at the conclusion of the experiment (Table 1), the time-series plots describe an approximate doubling of *H. erythrogramma* biomass (March to September 2013) at the northern site in uncleared nutrient-enriched plots (i.e. including both 'nutrient only:◆' and 'nutrient + sediment:✚' treatments). This increase in *H. erythrogramma* biomass was associated with the loss of all macroalgal cover (i.e. *E. radiata*, fucoids and understory cover) in these plots over the course of the experiment (Fig. 3e).

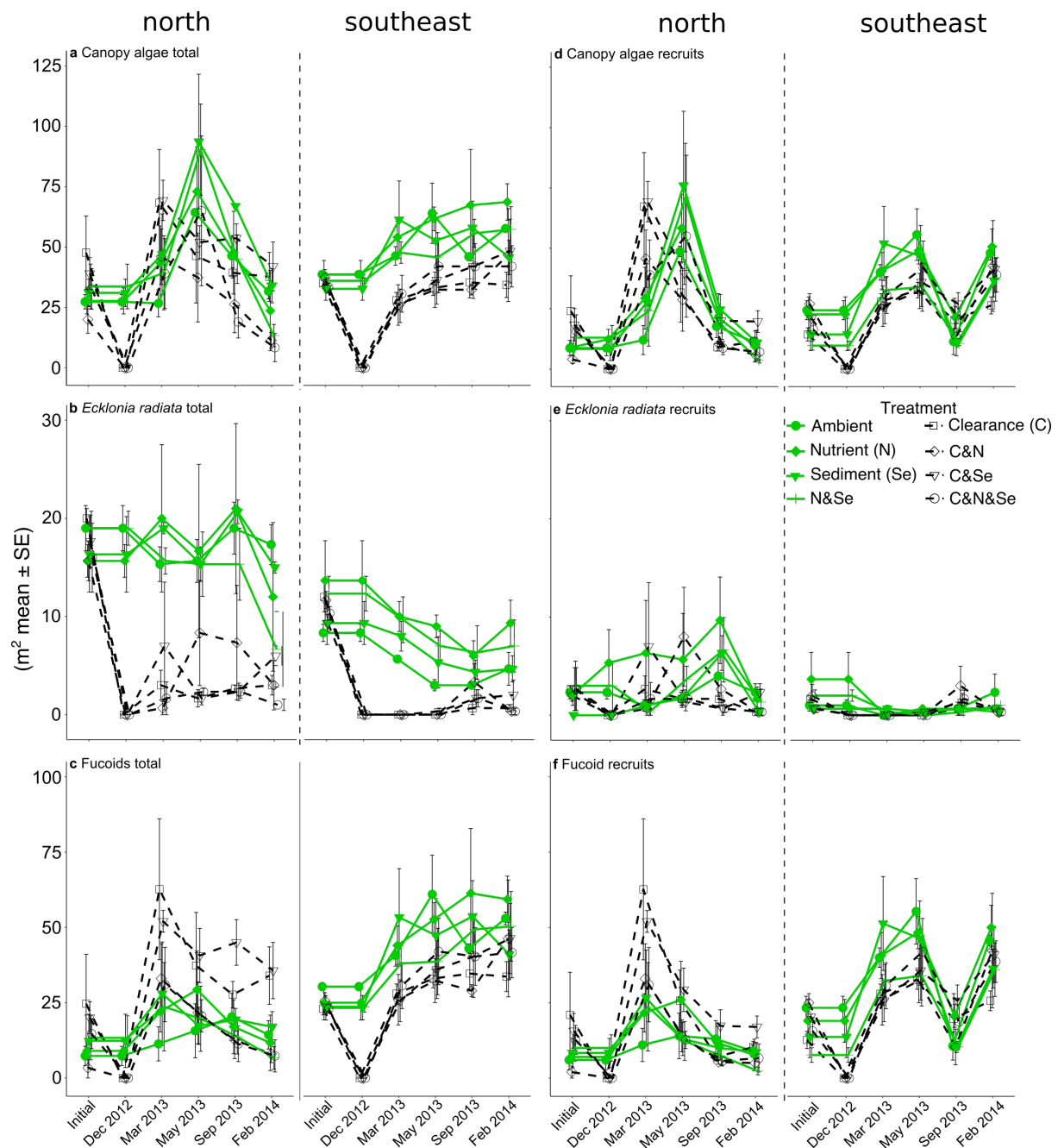


Figure 3. Mean sporophyte density ($\text{m}^{-2} \pm \text{SE}$) of a) total canopy-forming algae (including recruits and established sporophytes; see caption to Fig 2). Data are from $n = 3$ 1 m^2 experimental plots at two sites (north and southeast) where experimental plots were subject to all combinations of canopy clearance (uncleared versus cleared, indicated by green filled and unfilled symbols), nutrients (ambient versus enriched), and sediment (ambient versus elevated) treatments in an experiment ran for 15 months between December 2012 and February 2014.

Algal community response

PERMANOVA results show that differences among sites were the largest component of variability, with effect sizes (as ω_p^2) of 0.65 and 0.28 for the algal and faunal communities

respectively (Table 2). This pattern is evident from the CAP plot, showing distinct separation of north and southeast communities (Fig. 4ai and bi). Notably, the CAP (Fig. 4ai) also shows some separation of algal communities between the cleared and uncleared plots at the end of the experiment in the north. The striking outliers from this trend are the three elevated nutrient plots (N, N&Se) that are indistinguishable from the cleared plots. The separation between most of the cleared and uncleared plots is driven by a lack of canopy-formers, highlighting the lack of canopy resilience in the north. In contrast, the southeast shows less separation, representing the greater resilience of the canopy. The PERMANOVA suggest the algal communities were significantly differentiated by the combined effects of site, clearance and nutrients (S x C x N). Interestingly, cleared plots enriched with nutrients supported similar communities to cleared plots not enriched with nutrients (Table 2). Nutrients were also a significant factor differentiating the faunal community (Table 2), with nutrient enrichment resulting in communities of reduced richness at both sites (Table 3). There was nil effect of doubling of the sediment regimes (Table 1 and 3, Fig. 2).

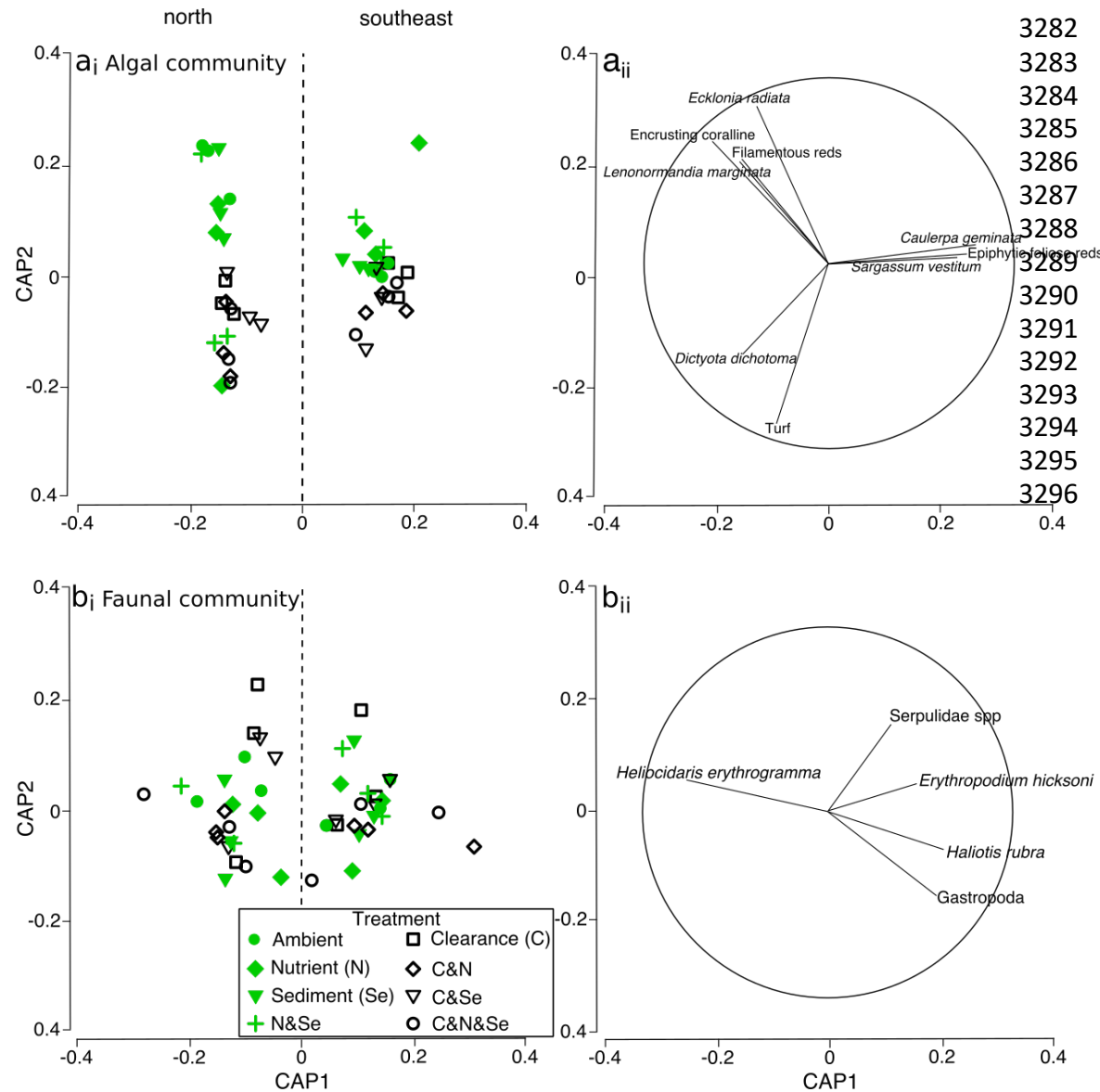


Figure 4. Ordinations from CAP (canonical analysis of principal coordinates) procedure on final abundances of a_i) algal community and b_i) faunal community. Dashed lines indicate the separation of plots grouped by site. Panels a_{ii} and b_{ii} show the associated vector plots identifying taxa contributing to the separation of groups (only Spearman correlations <0.5 are shown). Data are from n = 3 1 m² experimental plots where experimental plots were subject to all combinations of canopy clearance (uncleared versus cleared, indicated by green filled and unfilled symbols), nutrients (ambient versus enriched), and sediment (ambient versus elevated) treatments in an experiment ran for 15 months between December 2012 and February 2014.

3297

3298

3299 **Discussion**

3300

3301 This multifactorial manipulation of kelp canopy, nutrification, and sedimentation at two sites

3302 enabled assessment of multiple urban stressors on resistance-resilience dynamics of kelp

3303 beds. Shifts to turf and resilience of the laminarian *Ecklonia radiata* revealed additive effects

3304 of disturbance to canopy-formers and nutrification. However, this response was dependent

3305 on site and the starting state of the reef ecosystem (i.e. intact kelp beds *versus* cleared3306 'disturbed' beds). Local species pools and the differential effects of urchins on fucoids and *E.*3307 *radiata* appear to underpin the distinct differences in resistance-resilience dynamics among

3308 sites, and are important in the capacity for seaweed beds to maintain system stability under

3309 increasingly urbanised conditions, i.e. due to elevated sedimentation and nutrification.

3310

3311 ***Sea urchin biomass increase leads to contrasting resistance to elevated nutrients***

3312

3313 There were striking differences in the resistance dynamics between the two sites. The

3314 southeast showed resistance to urban stressors. In contrast, when nutrient was enriched, the

3315 northern site displayed low resistance. The reduced resistance was a result of increased

3316 *Heliocidaris erythrogramma* biomass density on nutrient-enriched plots supporting *E.*3317 *radiata*, resulting in these plots being overgrazed. Overgrazing of kelps and other seaweeds

3318 by this species causes sea urchin 'barrens' in PPB (Carnell and Keough 2016; Kriegisch et al.

3319 2016) and further afield in SE Australia (Valentine and Johnson 2005; Wright et al. 2005; Ling

3320 et al. 2010). It is possible that in the current study *H. erythrogramma* facilitated an indirect

3321 negative effect of nutrients on canopy algae by targeting nutrient enriched kelps. Other

3322 grazers have been shown to increase preferential consumption of nutrient-enriched algae
 3323 (Lotze et al. 2000; Bokn et al. 2003; Ghedini et al. 2015). Yates and Peckol (1993) found that
 3324 nutrient content was negatively related to polyphenolic content of tissue in *Fucus*
 3325 *versiculosus*. Individuals from a high nutrient site exhibited higher growth rates associated
 3326 with higher tissue nutrient, but lower phenolic content resulting in higher grazing rates of
 3327 nutrient-enriched algae over non-enriched algae by gastropods. Differential grazing of algae
 3328 has also been demonstrated and related to varying factors such as the life-stage of the algae
 3329 (i.e. recruit versus adult), level of chemical defences and overall availability of algae
 3330 (Steinberg 1989; Van Alstyne et al. 1999; Van Alstyne et al. 2001; Hill et al. 2003; Wright et al.
 3331 2005). In the southeast of PPB, furoid algae were more common than in the north, and
 3332 preferential grazing on *E. radiata* by *H. erythrogramma* and their avoidance of fucoids could
 3333 explain the continued decline of *E. radiata* throughout the experimental period and greater
 3334 persistence of fucoids.

3335

3336 ***Contrasting canopy resilience between sites***

3337 Experimental responses to manipulated ‘urban regimes’ revealed contrasting resilience of
 3338 kelp beds across sites. Following canopy removal, the reef at the northern site rapidly
 3339 became dominated by turfs, and the shift to turf was enhanced by increased nutrients (the
 3340 effects of canopy loss and elevated nutrients were additive). Once developed, turf
 3341 maintained spatial dominance for the remainder of the experimental period. This pattern is
 3342 consistent with dominance of turf algae in other regions in Australia (Gorgula and Connell
 3343 2004; Copertino et al. 2005; Carnell and Keough 2016) and elsewhere (Reed 1990; Strain et
 3344 al. 2014; Strain et al. 2015) when canopy-forming species are lost, and nutrients elevated.
 3345 Flow-on effects following proliferation of turf algae resulted in inhibition of recruitment of *E.*

radiata, but not furoid canopy-forming species (Table 3 and Fig. 3). In other studies, inhibition of recruitment of canopy-forming species by turfs has been linked to reduced settlement success and poor competitive capacity of early life-history stages of large brown seaweeds compared to turfs (Kennelly 1987; Reed 1990; Worm and Lotze 2006). However, I emphasise that the response of canopy-forming seaweeds to development of turf was species-specific, as while turfs inhibited recruitment of *E. radiata* (Fig. 3e), there was no detectable effect of turfs on furoid recruits following canopy removal (Fig. 3f). Notably, the fucoids did not recruit unless the *E. radiata* canopy had been cleared, indicating that fucoids are competitive subordinates to *E. radiata*, but more resilient to development of turf cover.

Site-dependent differences result from taxa-specific responses

While overall canopy cover was initially similar at both sites, the assemblage in the southeast was comprised of relatively species-rich canopy-forming and understory guilds. In contrast, the northern assemblage was a monospecific canopy of *Ecklonia radiata*, with a simple understory community composed largely of encrusting coralline algae (ECA). The strong association between ECA and *E. radiata* is consistent with observations from other studies across continental scales (Fowler-Walker and Connell 2002; Connell 2003; Irving et al. 2004). The *Ecklonia*-ECA complex is thought to result from a combination of strong direct and indirect effects of *E. radiata* sporophytes on the benthos (Kennelly 1989; Connell 2003). The thallus of *E. radiata* abrades the benthos when there is wave action, effectively scouring the benthos clear (Chapter 3; Wernberg et al. 2005), and acts to reduce light penetration (Kennelly 1989; Connell 2003). These direct and indirect effects positively affect the slowly-growing ECA which due to their prostrate form, calcium carbonate morphology, and photophysiology are less vulnerable to abrasion than turfs, invertebrates, and other erect

understory species, and better adapted to low light levels than many other seaweeds (Littler and Littler 1980; Kennelly 1989; Kendrick 1991; Steneck and Dethier 1994; Connell 2003). Thus, differences in the strength of interactions between dominant canopy-forming guilds (i.e. laminarian versus fucoids) can strongly influence the make-up of the constituent algal community, significantly influencing the identity of local species pools.

3375

The marked differences in resistance and resilience trajectories between our experimental sites can be explained by the differing species pools that characterise each site. In the case of turfs, our results suggest two possible mechanisms in southeast PPB which limit the development of dense algal turfs. First, fucoids were present to contribute to canopy development and resilience post-disturbance. Initially, I removed all canopy-forming species, however, fucoids may have propagated vegetatively from small amounts of remaining biomass as vestigial holdfasts (Schiel and Foster 2006), whereas the laminarian *E. radiata* must rely on sexual reproduction to re-establish. Additionally, fucoids have a simplified life-history compared to laminarians with no free-living gametophyte stage. This simplified life-history results in survival rates for fucoids several orders of magnitude higher than laminarians (Schiel and Foster 2006). Low survival from spore to gametophyte and a requirement of a threshold gametophyte density for effective fertilisation and sporophyte development means that sexual reproduction in kelps is complicated and risky compared to vegetative propagation (Chapter 2; McConnico and Foster (2005); Schiel and Foster (2006)). Second, the understory of the kelp bed in the southeast was diverse and occupied a significant proportion of the benthos, resulting in less available space for the turfs. In contrast, the northern community is composed of a species-poor understory community with high (~90%) cover of ECA, which are readily out-competed and overgrown by turfs (Kendrick,

1991; Airolidi, 2000; Reeves et al., 2017, unpublished). Thus, the southeast shows greater functional redundancy in its capacity to exclude turfs, derived from its species-rich canopy-forming and understory guilds. Our results indicate that the composition of the local community is an important factor in the resistance-resilience capacity of the system.

No effects of doubling of sediment load

A consistent result was the lack of a response to our experimental enhancement of sediments (doubling of ambient sediment deposition rates). This finding contrasts with a large body of literature that reports both significant negative direct and indirect impacts of elevated sediments on temperate reef biota (Devinny and Volse, 1978, Airolidi, 2003; Schiel et al., 2006; Strain et al., 2015) However, several other studies have also found limited effects of sediment addition (Ortega-Borges et al. 2009), or have even reported beneficial effects from elevated sediments (Roleda et al. 2008; Kawamata et al. 2012), indicating that the effects of sediments on algae can be complex. Many studies examining elevated sediment effects are laboratory-based and thus do not account for natural environmental conditions and variability (e.g. variable water motion), and these studies have predominantly identified strong negative impacts of sediments on macroalgae (Devinny and Volse 1978; Arakawa and Matsuike 1992; Schiel et al. 2006). Not surprisingly, when these studies are replicated in natural systems, the results of lab studies do not always hold (i.e. Schiel et al. 2006). Sediment flux on reefs in PPB is naturally high (Appendix 1a), and our study was conducted at relatively shallow depths (3 – 6 m), so the light was not limiting and the effect of water motion, at these depths, would likely influence the impact of sedimentation through resuspension. Development of algal turfs traps sediment to form a semi-consolidated turf-sediment matrix, while in areas dominated by *E. radiata* the kelps sweep the substratum and

3418 there is minimal sediment accumulation. Thus, both turf- and kelp-dominated communities
 3419 on shallow reefs in PPB have likely developed as sediment tolerant assemblages. It seems
 3420 clear that the action of water motion may moderate impacts of sediment in the natural
 3421 system studied here.

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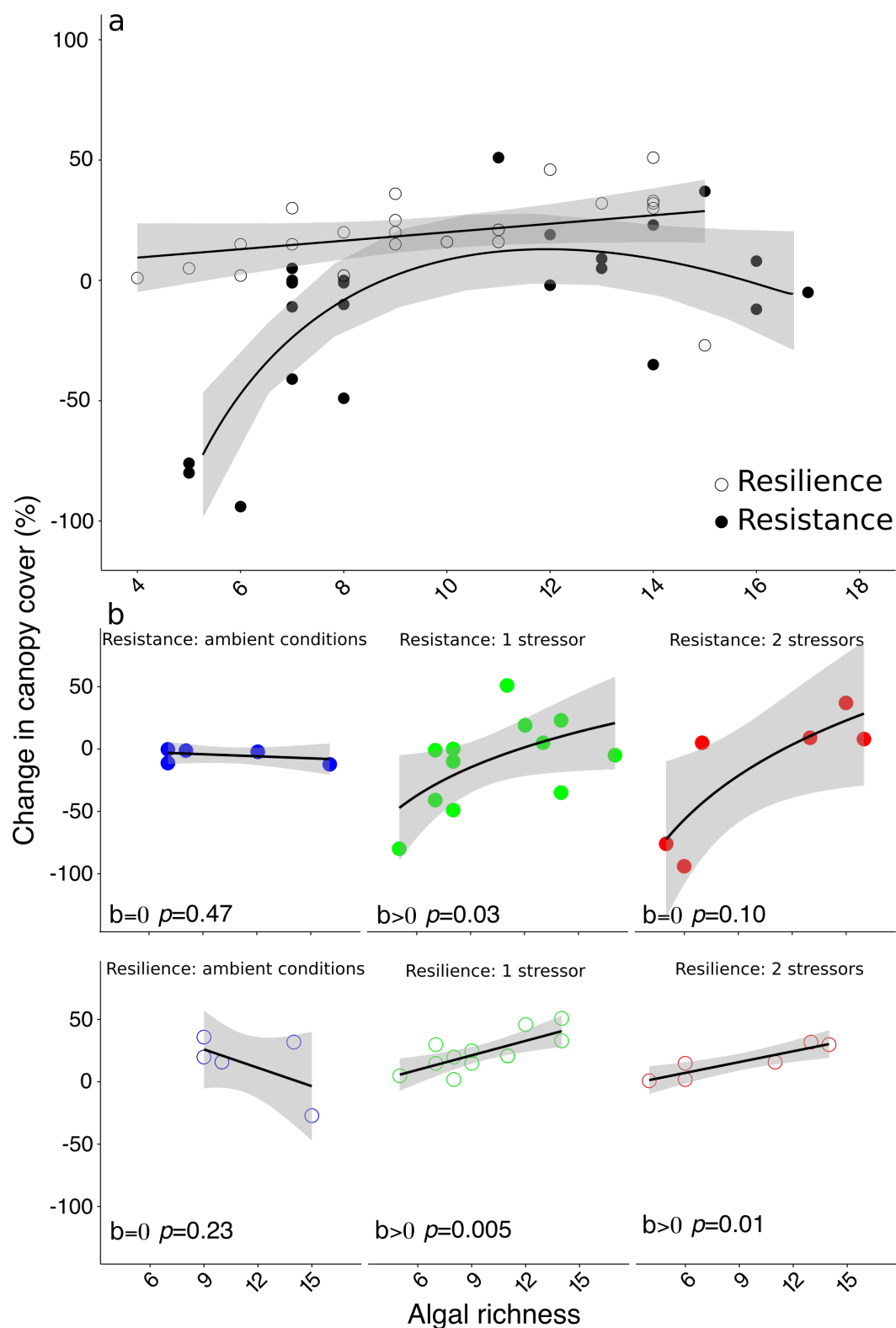
3423 *Kelp bed diversity and implications for restoration*

3424 For kelp beds in PPB to have the capacity to withstand (resistance) or recover (resilience)
 3425 from disturbance and multiple stressors, areas supporting a richer assemblage of canopy-
 3426 forming algae would appear to have an advantage over mono-specific canopies of *E. radiata*,
 3427 with loss of canopy cover less likely when the algal community is dominated by fucoids and
 3428 /or more species-rich (Fig. 5). Fig. 5 provides a conceptual model of resilience and resistance
 3429 to canopy loss and shows change in canopy cover as a function of the final species richness of
 3430 an experimental plot. Additionally, I used the multi stressor approach of the experiment to
 3431 split the data up to show resistance and resilience under ambient (0 stressors), one stressor
 3432 (sediments or nutrients singularly) and two stressors (sediments and nutrients combined).
 3433 In general, marine habitat restoration focussing on autotrophs has applied a monoculture
 3434 approach (Carney et al. 2005; Correa et al. 2006; Campbell et al. 2014; Williams et al. 2017).
 3435 This monospecific replanting relies on the ecological engineering capacity of the replanted
 3436 foundation species (*sensu* Dayton, 1985) (Williams et al. 2017). However, a monospecific
 3437 restoration attempt may not be a self-supporting system unless local stressors and
 3438 disturbances are ameliorated (Breitburg and Riedel 2005; Palmer et al. 2010; Johnson et al.
 3439 2017; Williams et al. 2017). With a monospecific kelp bed, if single or multiple stressors and
 3440 disturbances affects any aspect of that species' life-cycle, the bed may be vulnerable.
 3441 However, if there is a greater pool of species to form a restored/rehabilitated bed, then the

3442 likelihood of creating a self-supporting ecosystem that is resistant and resilient to
3443 perturbations is greater, as there is greater likelihood of another species/multiple species not
3444 being affected. This study indicates that kelp bed communities comprising mixed-species
3445 canopies, and a diverse understory, appear to increase functional redundancy and are better
3446 able to cope with multiple urban stressors. Whether this functional redundancy is imparted
3447 by the biological differences of fucoids in comparison to *E. radiata* (i.e. avoidance by urchins,
3448 greater recruitment capacity into turf areas and vegetative regeneration), or derived
3449 specifically from increasing algal richness, is difficult to distinguish. Nevertheless, kelp beds
3450 with mixed species canopies show greater resistance to shifts to turfs and increased
3451 likelihood of resilience following disturbance to canopy and to the multiple stress scenarios
3452 (sediments and nutrients) of urbanised coasts (Fig. 5). Caution should be used when
3453 generalising responses of kelp beds composed of single or multiple laminarian or fucoid taxa,
3454 as expecting all kelp beds to respond similarly may be a gross generalisation (Goodsell et al.
3455 2004) and responses of kelp beds to stressors and restoration may be more complex than
3456 anticipated. Restoration practitioners should aim to understand the proximate drivers that
3457 caused the need for restoration in the first place, and consider a multi-species approach to
3458 restoration, in effect diversifying risk across many species providing ‘ecological insurance’ to
3459 uncertainty from present and future stressors and disturbances (Elmqvist et al. 2003;
3460 Nyström 2006).

3461

3462



3463

3464 Figure 5. Measures of resistance and resilience of canopy-forming algae as a function of final algal
 3465 species richness (pooled across sites). a) Change in canopy cover with algal richness for cleared (o)
 3466 and uncleared kelp bed plots (●) (indicating resilience and resistance respectively). B) Change in
 3467 canopy-former cover with algal richness for cleared (o) and uncleared (●) kelp bed plots under
 3468 increasing stress regimes: 1 stressor = nutrient enrichment or sediment elevation; 2 stressors =
 3469 nutrient enrichment and sediment elevation.

3470 *Conclusion*

3471

3472 Our multi-factorial field experiment has highlighted variability in responses to urban stressors
3473 between localities. This study emphasises that caution should be used when attempting to
3474 generalise experimental results from a single site, and highlights the need to understand
3475 basic environmental and biotic feedbacks at a local scale before undertaking habitat
3476 restoration. Appreciation of local species pools, environmental conditions, and the
3477 differential susceptibility of canopy algae to stressors should considerably improve the
3478 success of any kelp bed restoration project. This research emphasises that restoration
3479 approaches may be more successful by restoring functional diversity rather than focussing on
3480 single species and that the concepts of resistance and resilience are not only important
3481 aspects of ecological theory but are also pertinent for practical restoration.

3482

3483 *Acknowledgements*

3484

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Appendices

Appendix 1. PERMANOVA analysis examining dissimilarity within algal and faunal communities on experimental plots allocated to treatment groups prior to application of experimental treatments.

Source	Algal community				Macrofaunal community		
	df	Pseudo-F	P(perm)	ω_p^2	Pseudo-F	P(perm)	ω_p^2
<u>Site (S)</u>	1	<u>44.17</u>	<u>0.00</u>	<u>0.48</u>	<u>16.65</u>	<u>0.00</u>	<u>0.25</u>
Clearance (C)	1	0.72	0.58	0.00	2.17	0.07	0.02
Nutrients (N)	1	0.78	0.54	0.00	0.86	0.51	0.00
Sediment (Se)	1	1.15	0.31	0.00	0.42	0.79	0.00
S x C	1	0.55	0.73	0.00	1.47	0.21	0.01
S x N	1	0.68	0.62	0.00	1.43	0.23	0.01
S x Se	1	1.04	0.39	0.00	0.78	0.56	0.00
C x N	1	0.42	0.80	0.00	1.55	0.20	0.00
C x Se	1	0.84	0.50	0.00	0.81	0.55	0.00
N x Se	1	0.46	0.78	0.00	0.82	0.55	0.00
S x C x N	1	0.86	0.49	0.00	0.81	0.54	0.00
S x C x Se	1	0.55	0.71	0.00	1.72	0.15	0.00
S x N x Se	1	0.66	0.63	0.00	1.34	0.27	0.00
C x N x Se	1	0.83	0.51	0.00	2.56	0.04	0.00
S x D x N x Se	1	0.36	0.84	0.00	0.28	0.88	0.00
Residual	32						
Total	47						

Notes: Analyses were on fourth-root and square-root transformed abundances for algal and faunal communities respectively, on Bray-Curtis similarity matrices and 9999 permutations. Degrees of freedom, pseudoF-values and permuted P-values are shown alongside the partialled effect size for each term as partial omega squared (ω_p^2). Significant terms are in bold, italicised and underlined.

3757 Appendix 2. Average abundances of species contributing to dissimilarity between experimental sites for a) algal and b) faunal communities surveyed prior to
 3758 experiment. Based on species contributions to sample (dis)similarities (SIMPER) analyses on fourth-root and square-root transformed abundances for algal
 3759 and faunal communities respectively, on Bray-Curtis similarity matrices.
 3760

a) Algal community dissimilarity between experimental sites

Species	north, mean abundance (percent cover)	southeast, mean abundance (percent cover)	Mean dissimilarity	Contribution to dissimilarity (%)	Cumulative contribution to dissimilarity (%)
Turf	2.07	55.55	4.56	8.12	8.12
Encrusting coralline algae	74.71	4.42	4.47	7.95	16.07
Foliose brown understory	0.00	1.94	3.46	6.16	22.23
Filamentous red	4.07	1.46	3.29	5.85	28.08
<i>Zonaria turneriana</i>	0.00	1.31	3.24	5.77	33.85
<i>Undaria pinnatifida</i>	0.60	0.00	2.58	4.59	38.44
<i>Acrocarpia paniculata</i>	0.00	0.60	2.57	4.58	43.02
<i>Sargassum decipiens</i>	0.00	0.35	2.30	4.10	47.12
<i>Caulerpa geminata</i>	0.00	0.39	2.23	3.97	51.09
<i>Lenormandia marginata</i>	0.15	0.14	2.2	3.93	55.02
<i>Exallosorus olsenii</i>	0.00	0.21	1.95	3.47	58.49
<i>Cystophora monilifera</i>	0.00	0.20	1.94	3.45	61.94
<i>Ecklonia radiata</i>	88.83	37.22	1.77	3.16	65.1
<i>Stenogramme interrupta</i>	0.14	0.00	1.72	3.07	68.17
<i>Lobophora bicuspidata</i>	0.00	0.14	1.72	3.06	71.22

b) Faunal community dissimilarity between experimental sites

Species	north mean abundance (m ²)	southeast mean abundance (m ²)	Mean dissimilarity	Contribution to dissimilarity (%)	Cumulative contribution to dissimilarity (%)
Serpulidae spp	0.05	4.62	10.98	21.77	21.77
Gastropoda	3.03	7.34	8.22	16.29	38.05
<i>Heliocidaris erythrogramma</i>	7.90	3.24	6.17	12.23	50.28
Porifera	0.79	1.14	5.12	10.15	60.43
<i>Erythropodium hicksoni</i>	0.00	0.74	4.56	9.04	69.48
<i>Tosia australis</i>	0.62	0.71	4.32	8.55	78.03

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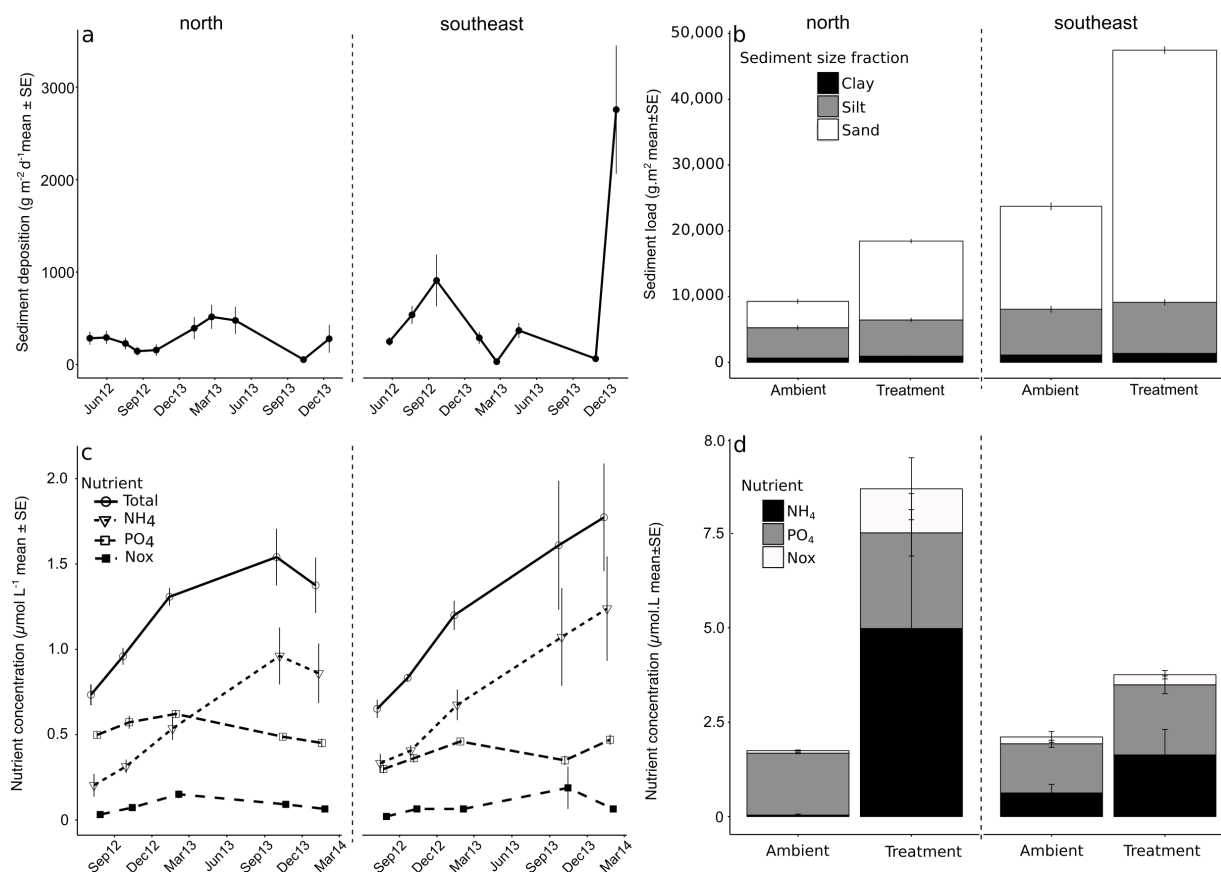
Appendix 3 PERMANOVA analysis examining the influence of nutrient enrichment (ambient versus enriched) and site (north versus southeast) on composite water nutrient concentrations. Analyses were on log+1 transformed dissolved nutrient concentrations ($\mu\text{mol L}^{-1}$), computed on Euclidean distance similarity matrices and 9999 permutations. Degrees of freedom pseudo-F values and permuted P -values are shown alongside the partial effect size for each term as partial omega squared (ω_p^2).

Source	df	Pseudo-F	P(perm)	ω_p^2
Treatment (T)	1	5.40	<u>0.02</u>	<u>0.16</u>
Site (S)	1	0.25	0.25	0.00
TxS	1	1.18	1.18	0.01
Error	20			
Total	23			

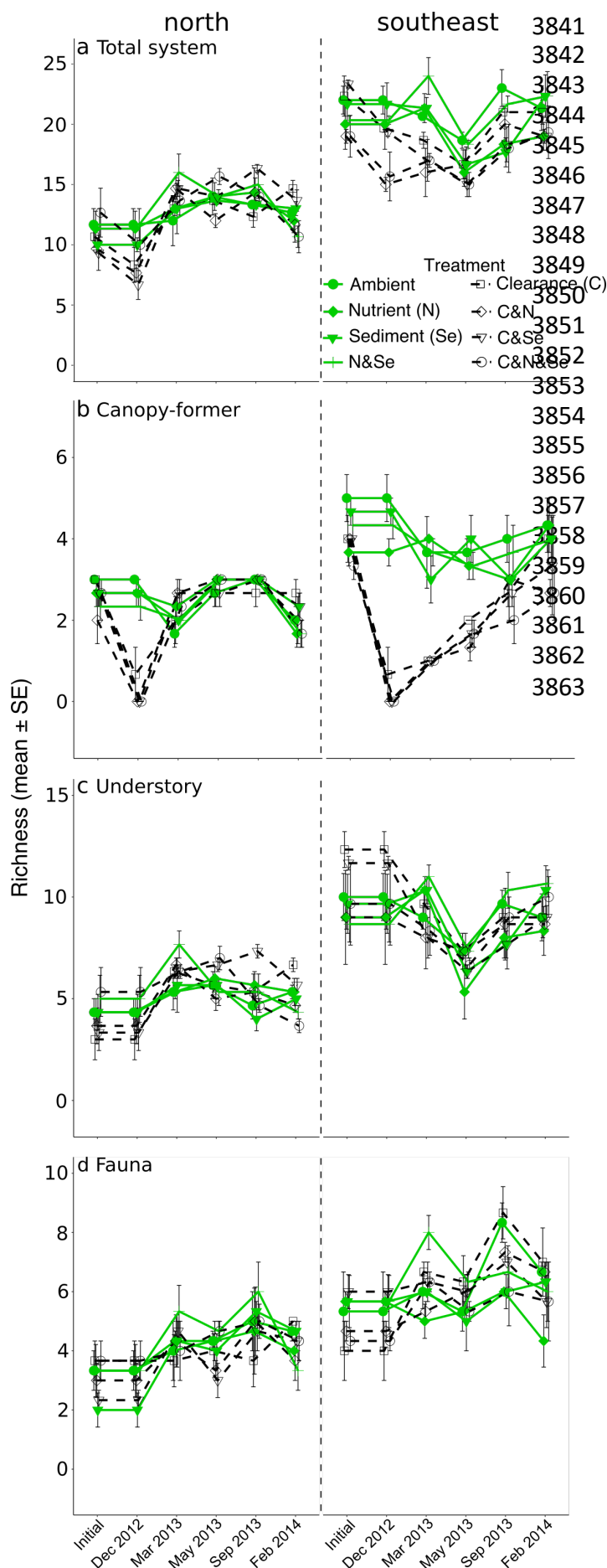
Appendix 4. Results of a four-factor model I ANOVA examining the influence of site (north (Nth) *versus* southeast (SE)), canopy-former clearance (uncleared (C-) *versus* cleared (C+)), nutrient enrichment (ambient (N-) *versus* enriched (N+)) and sediment elevation (ambient (Se-) *versus* elevated (Se+)) on richness of total community and key functional groups at the conclusion of the experiment.

Source	df	Total richness (Y) ^{0.4}		Canopy-former richness sqrt(Y)		Understory richness (Y)		Faunal richness (Y) ^{0.65}	
		F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2	F-value	ω_p^2
Site (S)	1	<u>157.7***</u>	<u>0.77</u>	<u>34.0***</u>	<u>0.41</u>	<u>145.33***</u>	<u>0.75</u>	<u>23.63***</u>	<u>0.32</u>
Clearance (C)	1	0.41	0.01	1.62	0.01	0.12	0.02	0.607	0.008
Nutrient (N)	1	<u>7.9**</u>	<u>0.13</u>	<u>4.4*</u>	<u>0.07</u>	2.32	0.03	<u>5.36*</u>	<u>0.083</u>
Sediment (Se)	1	0.04	0.02	1.10	0.00	0.67	0.01	0.122	0.019
S x C	1	2.45	0.03	5.05*	0.08	0.67	0.01	0.082	0.019
S x N	1	16.00	0.02	0.33	0.01	3.08.	0.04	0.058	0.02
C x N	1	0.34	0.01	0.87	0.00	0.67	0.01	0.285	0.00
S x Se	1	1.49	0.02	0.52	0.01	<u>9.97***</u>	<u>0.16</u>	0.036	0.021
C x Se	1	1.25	0.01	0.79	0.00	0.67	0.00	0.522	0.01
N x Se	1	0.05	0.02	0.18	0.02	0.12	0.02	0.522	0.01
S x C x N	1	0.59	0.01	0.37	0.02	2.32	0.03	0.324	0.014
S x C x Se	1	0.49	0.01	0.01	0.02	0.12	0.02	1.703	0.014
S x N x Se	1	0.00	0.00	0.57	0.01	0.67	0.02	0.088	0.019
C x N x Se	1	1.14	0.54	0.57	0.02	0.01	0.01	0.01	0.021
S x C x N x Se	1	0.24	0.17	0.18	0.02	0.12	0.02	2.711	0.034
Error	32								
Pair-wise tests									
S		SE>Nth		SE>Nth		SE>Nth		SE>Nth	
N		N->N+		N->N+				N->N+	
				SE:C-					
				>SE:C+>Nth:C-					
S x C				=NthC+					
						SE:Se+>SE:Se-			
S x Se						>Nth:Se+=Nth:Se-			

Notes: Variables examined in this analysis were the total community, canopy-former, or any algae of the Laminariales and Fucoiodes also including the canopy-forming invasive alga *Undaria pinnatifida*, understory algae defined as fleshy algae that are not canopy-formers and faunal communities both mobile and sessile. Transformations required to stabilise variances and maintain heteroscedasticity are detailed beneath the respective variable, F-values with indicators of significance are listed with partial effect sizes as partial omega squared (ω_p^2). For significant terms, the respective pair-wise analysis is detailed with significant groups separated by > and non-significant groups by =. In most instances, Tukey's honest-significant-difference (HSD) was used for pair-wise tests, however when overall ANOVA indicated significance, but Tukey's HSD showed no significant difference, Fisher's least-significant-difference (LSD) tests were used and indicated by underlined analysis. Significance codes: 0> '***' > 0.001> '**' > 0.01> '*' > 0.05> '.' > 1.



Appendix 5. Patterns in sediment deposition and nutrient concentrations. a) Mean sediment deposition ($\text{g m}^{-2} \text{d}^{-1} \pm \text{SE}$) at the north and southeast experimental sites from May 2012 to January 2014, sediment deposition was measured by $n=3$ sediment traps in each period at each site. (b) The sediment load for the treatment period (i.e. accumulated load over six weeks) in each sediment size fraction (Black: Clays; Grey: Silts and White: Sands). 'Ambient' represents the mean sediment size fraction load experienced at the two sites (2012 mean deposition, $n=5$ and $n=3$ sampling events for north and southeast respectively) 'Treatment' shows the load collected for the sediment treatment and the total describes the combined load experienced by elevated sediment treatments (Ambient + Treatment). (c) Mean nutrient concentration ($\mu\text{mol L}^{-1} \pm \text{SE}$) at the experimental sites from August 2012 to February 2013 ($n=3$ per sampling event). Nutrients sampled were total nitrogen oxides (Nox: Nitrite (NO_2^-) and Nitrate (NO_3^-)); Phosphate (PO_4^{3-}), measured as filterable reactive phosphate (FRP) and Ammonia measured as ammonium (NH_4^+); additionally, total nutrients was calculated (sum of all nutrients). (d) Total ambient and treatment nutrient conditions; colours represent the nutrients contributing to the total nutrient concentration (Ammonium: black, Phosphate: grey and total nitrogen oxides: white). Samples ($n=3$, of each nutrient elevation and ambient) were taken at three weeks through the six week treatment period to ensure maximum nutrient levels.



Appendix 6. Mean species richness (\pm SE) total system (all taxa algal and faunal; b) canopy-forming algae, any algae of the Laminariales and Fucoiodes also including the canopy-forming invasive alga *Undaria pinnatifida*; c) understory algae defined as fleshy algae that are not canopy-formers; d) fauna both sessile and mobile. Data shown detail time-series of variables (a-d) on (n=3) 1m² experimental plots for an orthogonal manipulative experiment undertaken at two sites (north and southeast) where experimental plots were treated to all combinations of canopy clearance (uncleared versus cleared), nutrients (ambient versus enriched) and sediment (ambient versus elevated) the experiment ran for 15 months between December 2012 and February 2014.

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3878 CHAPTER 5: Kelp bed edges define
3879 vulnerability to overgrazing, invasion and
3880 fragmentation to a turf-dominated state

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Abstract

Kelp beds form vital biogenic habitats in coastal regions of temperate seas worldwide. However, over past decades kelp decline has occurred along many coastlines, from cascading impacts leading to overgrazing, or in response to direct anthropogenic stressors. Here I use aerial photographs and field surveys to document a recent decline in native kelp beds in Port Phillip Bay (Victoria, Australia) between 2009 and 2015. Through a series of field experiments and surveys, I examine the drivers of kelp bed loss and fragmentation and investigate how the flow on effects of native kelp bed decline and fragmentation alters resistance and resilience of reefs to invasion by a non-native kelp (*Undaria pinnatifida*) and transition to a turf-dominated state. Kelp-loss and bed fragmentation increases the relative amount of kelp bed edges, i.e. edge-to-area ratio, of kelp patches, which accelerates decline by sea urchins (*Heliocidaris erythrogramma*) grazing patches from the 'outside-in'. Accelerated rates of patch loss happen when both 'outside-in' and 'inside-out' grazing co-occurs. Assays showed that urchin grazing and feeding behaviour changed across the kelp bed edge, with greater grazing rates and increased destructive grazing behaviour at the edge of patches. Recruitment and survival of kelps was limited in the edge areas, and turf cover increased where urchins overgrazed kelps. A combination of over-grazing and consequent uptake of space by turfs act to form a positive feedback loop that reinforces kelp bed decline; with overgrazing exacerbated by reduced provision of drift kelp. Ongoing kelp-loss, fragmentation and alterations to kelp bed dimensions, leading to increased edges, greatly erodes resilience to grazing and accelerates kelp bed collapse. This reefscape scale mechanism appears a vital consideration for effective restoration and management of kelp beds.

Introduction

Sub-tidal rocky reef habitats dominated by canopy-forming brown macroalgae (Laminariales, Desmarestiales and Fucales), broadly termed “kelp beds”, cover extensive areas of temperate coastlines worldwide (Dayton 1985; Steneck et al. 2002; Steneck and Johnson 2014; Krumhansl et al. 2016). The kelps are important foundation species, as they provide three-dimensional habitat structure, standing biomass and food for associated species (Dayton 1985; Ling 2008; Schiel and Lilley 2011). As biogenic habitats, kelp beds also influence local environmental factors such as water motion (Eckman et al. 1989; Jackson 1997; Wernberg et al. 2005), light (Kennelly 1989; Connell 2003; Wernberg et al. 2005), sediment accumulation (Eckman et al. 1989; Wernberg et al. 2005), and pH (Hofmann et al. 2011; Roleda et al. 2015; Britton et al. 2016). For these reasons, kelp beds support numerous ecosystem services, including commercial fisheries, nutrient cycling, and shoreline protection, valued in the range of billions of dollars annually (Smale et al. 2013; Bennett et al. 2016). It follows that changes to kelp populations will have significant consequences for reef community dynamics and provision of ecosystem services.

Occupying the temperate coastal zone of all continents except Antarctica, kelps are directly exposed to many stressors relating to human activities (e.g. harvesting, pollution, sedimentation, invasive species, recreation) (Steneck et al. 2002; Bennett et al. 2016). Historically, kelp habitats have been considered highly resilient (Dayton et al. 1984; Kennelly 1987b; Kennelly 1989; Dayton et al. 1992), but a number of recent studies have shown that the capacity of kelps to recover post disturbances has been eroded (Chapters 2 and 4, Gorgula and Connell 2004; Coleman et al. 2008; Perkol-Finkel and Airoidi 2010; Johnson et al. 2011; Strain et al. 2014; Ling et al. 2015). Reconstructing historical baselines and dynamics

over past decades has revealed distinct reductions in cover of macroalgal habitats in some places (Johnson et al. 2011; Krumhansl et al. 2016). Loss of kelp beds has distinct flow-on effects, including reducing structural complexity and biodiversity (Folke et al. 2004; Ling 2008; Stuart-Smith et al. 2015), and unwanted phase-shifts to reef systems dominated by ephemeral annual algal species (Airoidi and Cinelli 1997; Eriksson 2002; Valentine and Johnson 2003; Gorman and Connell 2009; Strain et al. 2015).

A primary driver of kelp-loss in many systems is herbivory (Poore et al. 2012; Ling et al. 2015). Herbivory is a fundamental process in all ecosystems; as a significant mechanism for transfer of primary production to higher trophic levels, and can affect the structure, abundance and productivity of vegetated habitats (Vanderklift and Wernberg 2008; Poore et al. 2012). Quantifying the impacts of herbivory on primary producers, and the relative strength of interactions between predator and prey is vital to understanding the role of consumer control in driving kelp loss. Collapse from a productive kelp bed to sea urchin-dominated ‘barren grounds’ largely devoid of seaweeds (Lawrence 1975; Ling et al. 2015) typically reflects a trophic cascade; overharvesting reduces predators (e.g. sea-otters, lobsters or fishes), that feed on urchins, so that urchins increase in abundance to the point where they destructively overgraze kelps (Estes and Duggins 1995; Steneck et al. 2002; Ling et al. 2009; Steneck and Johnson 2014). Other stressors can exacerbate kelp loss by altering biological interactions (i.e. predation, competition or facilitation) (Crain et al. 2008; Wernberg et al. 2013; Strain et al. 2014). On urbanised temperate coasts, there is concern about the permanent replacement of kelps with opportunistic taxa such as turfs (Worm and Lotze 2006; Airoidi et al. 2008; Gorman and Connell 2009,). The replacement of kelp ‘forests’ with ‘turfed’ landscapes is a consequence of the physiology of algal opportunists (i.e. rapid

vegetative growth and ability to tolerate elevated sediments) that usually enables normally competitive subordinate turf algae to persist in human-dominated seascapes characterised by elevated nutrients (Eriksson 2002; Worm and Lotze 2006; Filbee-Dexter and Wernberg, 2018; O’Brien and Schiebling 2018) and sedimentation rates (Gorgula and Connell 2004, reviewed by Airoidi 2003). Both singly and in combination, these stressors can cause strong feedbacks to affect the local structure and function of reefs, which can manifest at seascape scales (Ling et al. 2009; Marzloff et al. 2011; Steneck and Johnson 2014; Strain et al. 2014).

Degradation at the level of seascapes manifests as habitat loss and fragmentation. The former being a reduction in the total amount or the proportion of habitat occupied within the seascape, while the latter refers to the breaking apart of large, continuous patches into smaller units (McGarigal et al. 2005; Santos et al. 2016). Studies of marine habitat loss and fragmentation are relatively rare and usually only examine the impact of habitat fragmentation on biodiversity, ignoring flow-on effects on composition, connectivity and ecosystem dynamics (Andren 1994; Goodsell and Connell 2002; Coleman and Kelaher, 2009; Macreadie et al. 2009; Warry et al. 2009; Deza and Anderson 2010).

Here I combine understanding of local (metre scale) processes with landscape patterns and processes to 1) document fragmentation and habitat loss of native kelp, and 2) examine the impact of changing kelp bed patch-size on the functional role of native kelp on rocky reef ecosystems dynamics. This multi-dimensional approach enables both recognition of spatial and temporal habitat changes and identifying feedbacks from kelp-loss that affects the resilience of seaweed-dominated reefs.

3993 **Methods**

3994 *Study Site*

3995 This research was undertaken on rocky reef in the north of Port Phillip Bay (PPB), adjacent to
 3996 Williamstown Beach (hereafter Williamstown; S 37° 52' 10.5564", E 144° 53' 36.4884"), 10
 3997 km from the urban centre of Melbourne, Australia (population ~5M; Fig. 1a). The
 3998 Williamstown reef is contiguous from mean low water (MLW) to 5 m depth (width 150-200 m
 3999 from MLW) where it grades to silty sand. The reef is conglomerate boulder and cobble
 4000 basaltic rock (Bowler 1966), interspersed with small patches of sand (Fig 1b). Native kelp
 4001 *Ecklonia radiata* [(C. Agardh) J. Agardh 1848, Family: Lessoniaceae] occurs as small remnant
 4002 beds ($10 - 10^3 \text{ m}^2$), seen as dark patches in Fig. 1b. The introduced annual Japanese kelp
 4003 *Undaria pinnatifida* [(Harvey) Suringar, 1873, Family: Alariaceae] also occurs in dense small
 4004 stands forming a closed canopy covering ~0.5–1 m² (4-20 individuals per patch) on the urchin
 4005 barrens and in the ecotone between barrens and native kelp bed habitat. *U. pinnatifida*
 4006 occurs as large ephemeral beds in the west of PPB where it has established longest (Campbell
 4007 and Burridge 1998). Turf algae manifest as a semi-consolidated matrix of filamentous
 4008 epilithic-algae sediment matrix, here-after termed "turf", composed of filamentous
 4009 Rhodophyta, Chlorophyta and Ochrophyta taxa that trap sediments. This turf is distinct from
 4010 turfs lacking bound sediments or those comprised of articulated coralline algae (e.g. Connell
 4011 2003). The Williamstown reef is dominated by the sea urchin *Heliocidaris erythrogramma*
 4012 (Valenciennes, 1846; Family: Echinometridae), which forms and maintains sea urchin barrens
 4013 seen as pale dappled areas in Fig. 1b. The urchin barrens are characterised by bare-rock
 4014 and/or high cover of corallines and sediment-trapping turfing algae that form a continuous
 4015 network among the remnant beds of *E. radiata*.

4016

4017 *Identification of kelp patches*

4018 Putative kelp beds were first identified using the historical image library in Google Earth Pro,
4019 version 7.3.0 (<https://earth.google.com/download-earth.html>). These kelp beds were then
4020 ground-truthed by SCUBA diver towing a logging GPS around the perimeter of the kelp beds.
4021 Purchase of a *Nearmap Ltd* (<https://www.nearmap.com.au/>) license provided access to high
4022 resolution, regularly updated, aerial PhotoMaps of Australian cities and towns including the
4023 north of PPB. The PhotoMaps incidentally captured the nearshore benthic environment, and
4024 on days when environmental conditions permitted (i.e. lack of glare and no wind driven
4025 swell) high-resolution images of the nearshore subtidal reef habitats were captured (for
4026 example see Fig. 1b). A Nearmap library of high-resolution PhotoMaps was collated for the
4027 study area of Williamstown. Nearmap MapBrowser was used to precisely measure area,
4028 perimeter, and fragmentation of ground-truthed kelp beds through time.

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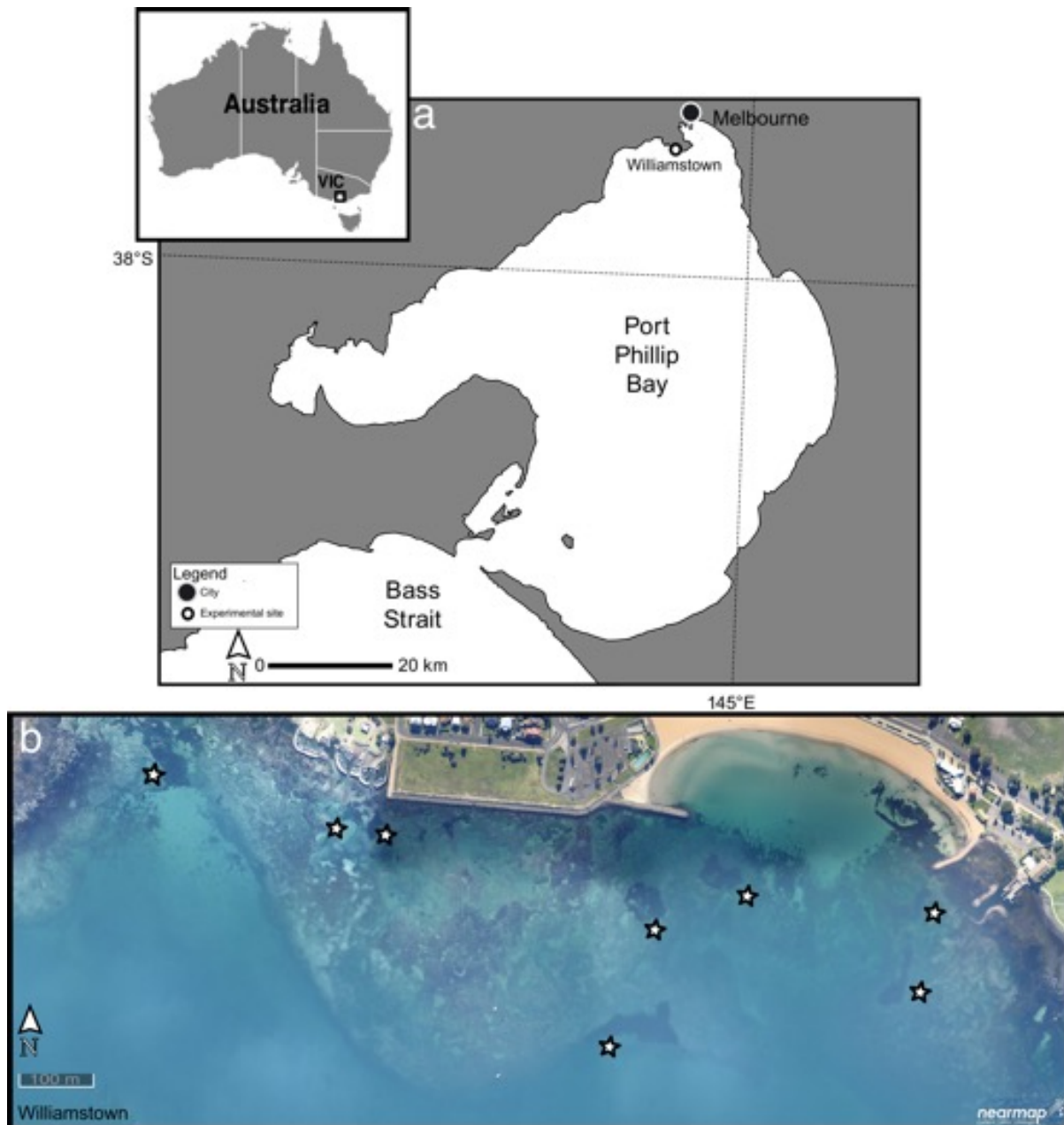
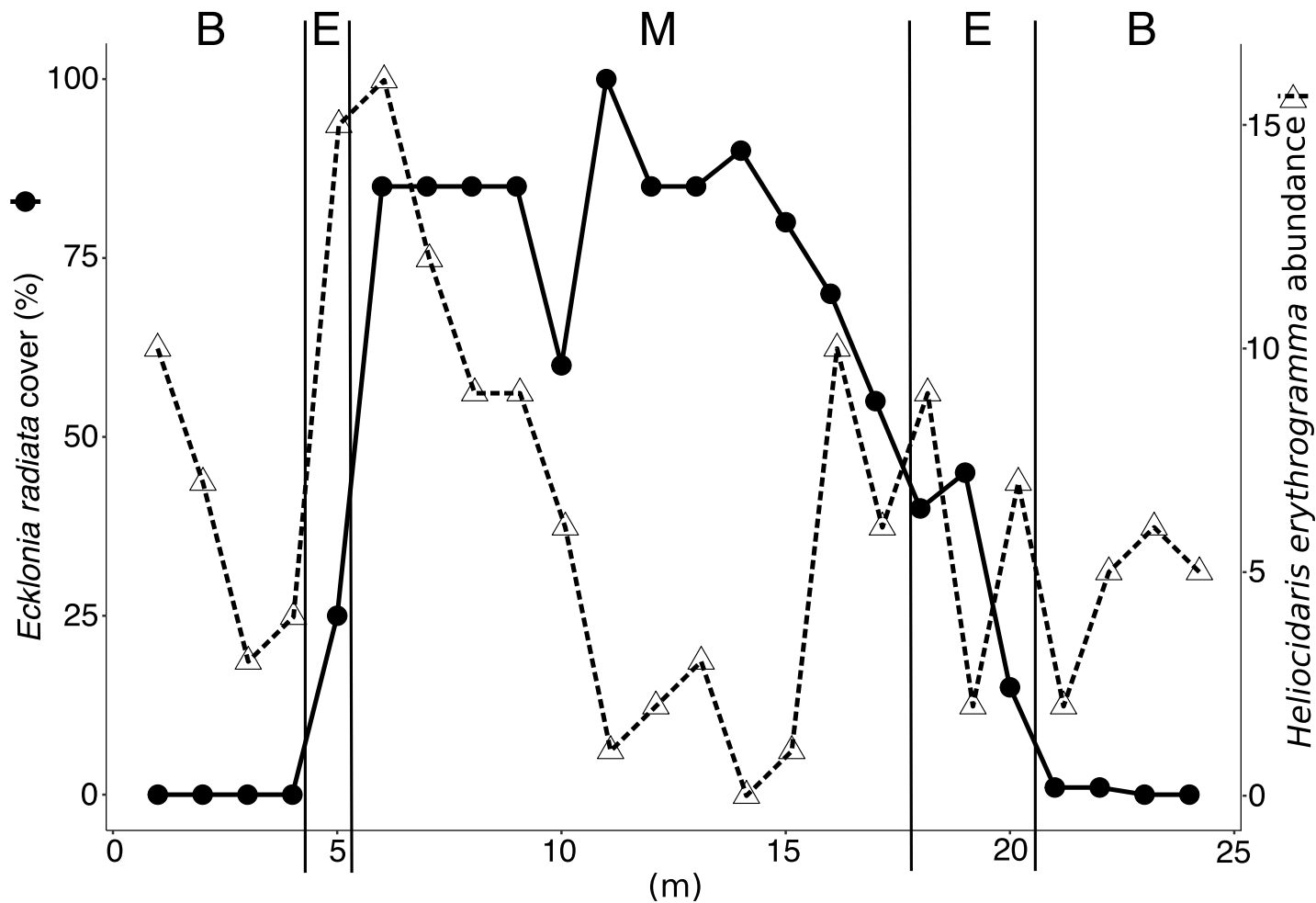


Figure 1. a) Map of the study location in Port Phillip Bay, an urbanised embayment in southeastern Australia, the location of the cities Melbourne and Geelong (large symbol, bounded in white) in relation to the Williamstown site (small white symbol, bounded in black) are shown, dark polygons depict the urbanised extent of the cities; b) The Williamstown study site showing the dark remnant kelp beds surrounded by lighter urchin barren reef (mottled) grading to silty sand. White stars are alongside remnant kelp beds (Nearmap, 5 September 2014, Williamstown, Australia, <http://maps.au.nearmap.com/>).

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4039 Figure 2. Example cross-section through a kelp patch showing middle, edge and barrens zones. *Ecklonia radiata* percent cover (solid line and filled
4040 black circle) and *Heliocidaris erythrogramma* abundance (dotted line, open triangles) through a kelp patch. Kelp patch zone categories are defined
4041 by their cover of *E. radiata*: 0% < Barren (B) ≤ 5%, 5% < Edge (E) ≤ 45%, Middle (M) > 45%.
4042

Characterisation of zonation in kelp beds

For ground-truthed kelp patches, in situ belt transects (varying lengths dependent on size of patch) of contiguous 1x1 m quadrats were run across the beds and assessed by SCUBA divers. Assessment of each quadrat included recording percentage cover of reef substratum types, classification comprised flat rock shelves (>5 m effective diameter); the presence of cracks or crevices was noted, very large boulders (>2.5 m and < 5 m diameter), large boulders (>1 m and <2.5 m diameter), small boulders (>0.2 m and <1 m diameter), cobble (>0.1 m and < 0.20 m diameter), pebble (>0.01 m and < 0.10 m diameter), gravel (< 0.01 diameter), or sand. Additionally, percentage cover of all algae and counts of the laminarian kelps *Ecklonia radiata* (as per Kirkman 1981) and invasive *Undaria pinnatifida* (defined as: Stage I individuals that are teardrop to oblong in shape with no pinnae or midrib, Stage II individuals have a midrib and developed or developing pinnae, but no sporophyll, Stage III individuals are fully developed with pinnae and sporophyll) and furoid species (*Cystophora monilifera* and *C. moniliformis*, *Sargassum vestitum*, *S. decipiens* and *S. fallax*) were assessed. For the furoids juveniles were defined as thalli with low lying basal leaves and no evidence of axes, floats or receptacles; while adults showed evidence of axes (even if regressed) and receptacles and floats when reproductive. I also quantified percentage cover and depth of the turf. Five replicate measurements were made by pushing a metal ruler perpendicularly into the turf until it contacted hard substratum. One measurement was taken in each of the 0.25 m² segments of the full 1 m² assessment quadrat, plus an additional random point. Sessile and mobile invertebrates I also assessed, including the urchin *H. erythrogramma*, which is known to overgraze and create extensive sea urchin barren in PPB (Constable 1990; Carnell and Keough 2016; Kriegisch et al. 2016). Urchin density was converted to biomass using the

relationships of Kriegisch (2016). Urchin biomass was calculated by using the allometric relationship between test diameter and fresh weight determined for Williamstown (determined from $n = 60$ urchins). Urchin density was converted to biomass density from the test diameter of $n = 10$ randomly collected urchins. Note that because of the non-linear relationship, the allometric equation was used on each urchin individually to estimate individual biomass, and then the average of these biomasses was utilised. In total, nine kelp patches were sampled in situ. Clear increases in *H. erythrogramma* abundance were observed alongside distinct declines in kelp cover, and these areas were defined as “Barren”, less than 5% cover of kelps; Edge (E), canopy cover between 5% and 45%; and Middle (M) with canopy cover $\geq 45\%$ was developed (Fig. 2).

In situ surveys and experiments

In October 2014, three kelp patches with similar perimeter and area characteristics were selected. According to the kelp bed zonal classification, ten random 1 x 1m quadrats were assessed within each of two replicate 10 x 25 m grids in each of the Barren, Edge and Middle zones. Linear mixed models (LMM) were used to examine zonal differences in biomass of *H. erythrogramma*, *E. radiata* recruitment (Stage I abundance), turf abundance and *U. pinnatifida* abundance.

Sea urchin grazing rates

Grazing rate assays followed a simplified methodology after Vanderklift and Wernberg (2008) and Vanderklift et al. (2009). Standard lengths (200 mm) of the kelp *E. radiata* were anchored in two arrangements to simulate differing supplies of kelp resource. I measured the relative consumption of detached (drifting) *versus* attached kelp using treatments to mimic both. To mimic drifting detached kelp, I fastened a clothes peg to a piece of kelp, and tied the peg to one end of a length of nylon fishing line (500 mm). The drift kelp mimic was anchored

4094 to a short (50 mm) length of chain (5mm welded short link chain) allowing the kelp to drift
 4095 over the reef with water motion. Attached kelp was mimicked by kelp pieces clipped to
 4096 clothes pegs, oriented to mimic upright reef attached kelps and anchored to lengths of chain
 4097 as described previously. The chain in both treatments was nestled amongst the substrate to
 4098 avoid any confounding affects from the added structural complexity contributed by the
 4099 chain. Kriegisch (2016) used two further treatments to partition grazing between sea urchins
 4100 and fish, and natural erosive processes in PPB. Caged algae were used to protect the algae
 4101 from consumption by fish and urchins, floating kelp pieces at canopy height (250 – 300 mm
 4102 above the substrate) were used to examine consumption by fish. The only putative algal
 4103 feeding fishes noted at the site were *Girella zebra* (Richardson, 1846) and *Parma victoriae*
 4104 (Günther, 1863); in ~ 4 years diving intensively at this site, I have never observed these fishes
 4105 feeding on attached or drifting *E. radiata*. Over the period of 3 days, zero fish herbivory or
 4106 erosion of kelp was recorded (Kriegisch 2016). Each treatment had 12 replicates (24 pieces of
 4107 algae in total) and was set up in the three zones of the 3 kelp beds; the assay was run for
 4108 three days as per Vanderklift and Wernberg (2008), Vanderklift et al. (2009) and Kriegisch
 4109 (2016). All *E. radiata* sections were pressed between two sheets of transparent Perspex and
 4110 photographed, before and after the experiment, and any change in area was calculated using
 4111 Image-Pro Plus Version 6.3 (Media Cybernetics, Bethesda, Maryland, USA). To convert rates
 4112 of change in area to rates of change in biomass, 10 (200 mm) algal pieces from each kelp bed
 4113 were photographed and weighed (both fresh [1.77 ± 0.10 , mean \pm SE] and dry weight
 4114 determined by drying at 80°C for 48 hours or until constant weight (0.15 ± 0.02) was
 4115 achieved). From this the relationship between blade area and biomass was derived, and used
 4116 to calculate total (g d^{-1}) and per-capita (g urchin d^{-1}) grazing rates in each zone. Linear mixed

models (LMM) were used to examine differences in grazing rate due to ‘zones’ (i.e. Barren, Edge and Middle) and the ‘source’ of algal resource (i.e. attached or drift).

***E. radiata* survival assay**

Survival of *E. radiata* life-stages in each zone was assessed in the three kelp patches. Four Stage I, II and III *E. radiata* were tagged in each zone and following one month the survival of sporophytes were assessed. The effect of zone (3 zones; Barren, Edge and Middle) and life-stage of *E. radiata* (3 life-stages; Stage I, II and III) on the percentage survival of *E. radiata* was assessed using an LMM.

Statistical analysis

To evaluate differences between zones within the three kelp patches, I fitted either a linear mixed model (LMM-Gaussian) or a generalised linear mixed model (GLMM-Poisson) as appropriate where the intercepts were varying or random, in other words the model assumes a different intercept for each level of the random factor. For all analyses ‘patch’, a random factor, accounted for environmental variability among patches. All analyses used R version 3.1.2 (R Development Core Team 2015) running in RStudio version 1.0.136 (RStudio Team 2015). LMM and GLMM analyses were undertaken using the package ‘lme4’ (Bates et al. 2006). I tested for fixed effects only using a parametric bootstrap function (Hertzog 2015) from the package ‘pbrktest’ (Halekoh and Højsgaard 2014). This function simulates data (the response vector) from the null model, then fits these data to the null and full model and derives a likelihood ratio test (LRT) for each of the simulations. The observed LRT is then compared to the null distribution generated from many simulations and a p-value estimated. The advantage of using this approach over considering p-values from a chi-square test on the LRT, is that in the parametric bootstrap I do not assume any null distribution but derive our null distribution from the model and the data at hand (Hertzog 2015). The R package

4142 'lsmeans' (Lenth 2016) was utilised to run *a posteriori* multiple comparisons for significant
4143 effects.

4144 Reef substrata complexity has been shown to affect sea urchin grazing, due to greater
4145 provision of refuges for urchins (Andrew, 1993; Benedetti-Cecchi and Cinelli, 1995; Spyksma
4146 et al. 2017). The substrata types that provide the greatest amount of refuge for urchins are
4147 large (>1 m and <2.5 m diameter) and small boulders (>0.2 m and <1 m diameter). I
4148 hypothesise that if reef substrate type is contributing to drive urchin grazing and kelp patch
4149 formation, then a greater percentage of large and small boulders would be expected in zones
4150 that are becoming/have become urchin barrens i.e. Barren and Edge vs. Middle. Reef
4151 substrate type was analysed by PERMANOVAs and SIMPER (using PRIMER-E V7 with
4152 PERMANOVA add-on Clarke and Gorley 2015). To evaluate differences between zones within
4153 the three kelp beds, I fitted a PERMANOVA with 'Zone' as a fixed factor and 'Bed' as a
4154 random factor. Percent cover of substrate type was untransformed and PERMANOVAs were
4155 computed on Euclidean distance matrices using 9999 permutations and unrestricted
4156 permutations of raw data to generate P-values. Type III sums of squares were used and
4157 permutational post-hoc t-tests were used to test pair-wise combinations of groups for
4158 significant effects (Clarke et al. 2014). P-values were obtained by Monte-Carlo tests (Clarke et
4159 al. 2014). SIMPER analysis was used to identify substrate type that accounted for observed
4160 differences in percent cover of substrate types for significant factors. Non-metric MDS
4161 (nMDS) and bubble plots were used to visualise any separation of groups additionally, vector
4162 plots (based on Spearman correlations with a threshold $R>0.5$) were overlayed over nMDS
4163 ordinations to examine substratum type most associated with separation.

4164

Results

Reefscape level changes to kelp bed dynamics

During the seven-year period between 2009 and 2015, 17,822 m² of kelp bed of *Ecklonia radiata* was lost from Williamstown (Fig. 3a). Concomitant with this fragmentation of habitat was an increase in the ratio of perimeter-to-area of the kelp patches (dashed line – Fig. 3a) although the rate of kelp loss was not consistent among patches (Fig. 3b). The greatest rate of kelp loss was observed between 2009 -2011 (Fig 3a), this was particularly evident for the patch illustrated in Figure 3d. The rate of kelp loss reduced once there was relatively little kelp remaining additionally the change in perimeter-to-area ratio stabilised (Solid line with square symbols – Fig. 3b-d).

Sea urchin biomass

Biomass density of the urchin *H. erythrogramma* was highest in the edge zone (563.2 g m⁻² ± 101.24, mean ± SE), followed by the barren zone (334.91 g m⁻² ± 168.09), while the middle of kelp patches supported the lowest biomass (195.68 g m⁻² ± 52.42) across all kelp patches (Fig. 4b, Table 1).

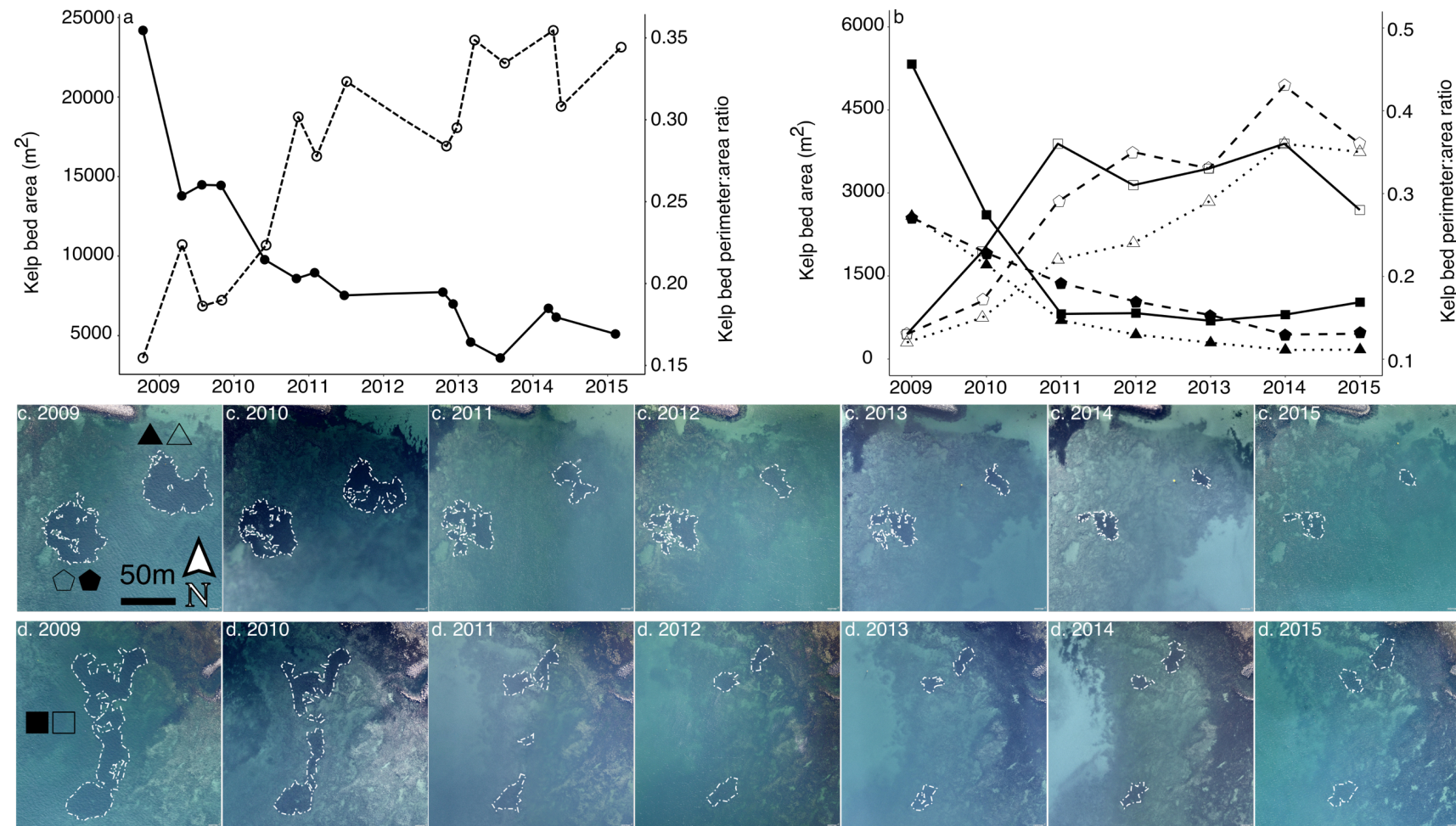


Figure 3. Kelp bed dynamics at Williamstown, 2009 to 2015. a) Area of all kelp patches at Williamstown (solid line and circles, m^2) and total perimeter-to-area ratio (dashed line and open squares). b) The trend in kelp bed area loss and increases in perimeter to area ratios for three example beds shown as maps in c) and d), symbols representing each kelp bed are consistent between panels b-d; dotted white lines depict patch boundaries. All aerial photographs were taken in the Austral winter and spring (Nearmap, Williamstown, Australia, <http://maps.au.nearmap.com/>).

Sea urchin grazing rates

Attached and drift *E. radiata* were grazed at different rates in the different zones of the kelp patches. Grazing rates were highest on urchin barrens regardless of the source of kelp availability (Fig. 4a and Table 1). As attached kelp became more available (i.e. progressing into the middle of the bed), grazing rates on drift kelp was higher than grazing rates of drift in the barrens (Fig. 4a and Table 1). Conversely, grazing rates of attached kelp were highest on urchin barrens, then reduced progressively into the interior of the kelp beds (Fig. 4a and Table 1). Per-capita grazing rates on both attached and unattached kelp were lowest in the edge compared to barrens and middle zones.

Macroalgal dynamics

Kelp recruitment and survival

The occurrence of *E. radiata* stage I sporophytes was greatest in the middle of the kelp bed and diminished towards the edge of the patch into the barrens (Fig. 4c, Table 1). A similar pattern was observed for kelp survival, with survival decreasing from the middle of kelp patches to the edge and into barrens. The probability of kelp survival was similarly low between the edge and barrens zones, and increased to 75 – 100% survival for Stage I, II and III sporophytes in the middle of kelp beds (Fig. 4d, Table 1).

Invasibility by turfing algae and exotic kelp

Cover of turfs was indistinguishable between the barren and edge zones (Barren: 80.7 ± 30.24 and Edge: 68.83 ± 19.19), but significantly lower in the interior of the kelp beds (Middle: 13.46 ± 15.6) (Fig. 4d, Table 1). A similar pattern was observed for the invasive kelp

4221 *U. pinnatifida*, with lower abundances of the invasive in the interior of the kelp bed
4222 compared to the Barren and Edge zones (Fig. 4d, Table 1a).
4223
4224
4225 *Similarity of substrate type within patches*
4226
4227 The substrata within the patches in northern PPB was composed of large to small boulders
4228 (2.0 to 0.2 m in diameter) (Fig. 5a and b). The PERMANOVA (Table 2) suggests that there are
4229 differences of substrate type with zones in beds. Pairwise tests show that this difference is
4230 driven by the ratio of small and large boulders observed in edge vs. barren and middle zones
4231 for bed I. Whilst for bed III flat rock, very large boulder are greater in the middle whilst small
4232 boulder is greater in the edge zone. It is evident that substrate type differences are not
4233 consistent between zones of kelp beds at Williamstown, therefore I think it would be
4234 challenging to justify that substrate may be driving the consistent patterns of urchin grazing
4235 observed across kelp bed zones in this experiment.
4236
4237

4238 Table 1. Results of linear mixed effects (LMM) and generalized linear mixed effects models (GLMM) of a 2-way design testing kelp bed zones (3 levels: barren
 4239 (B), edge (E) and middle (M)) on *Heliocidaris erythrogrmma* biomass, Turf-sediment matrix cover, abundance of *Ecklonia radiata* recruits, and *Undaria*
 4240 *pinnatifida* and 3-way designs testing *E. radiata* life stage (3 levels: Stage I, II, and III), and kelp bed zone on survival (%) of *E. radiata* sporophytes; and kelp
 4241 source (2 levels: drift and attached) and kelp bed zone on *H. erythrogrmma* grazing rate. For both the 1-way and 2-way cases patch was fitted as a random
 4242 effect within the model. Degrees of freedom, likelihood ratio test (LRT) values and a posteriori multiple comparisons for significant effects. Results only
 4243 shown for fixed factors of interest. Significant effects are indicated by asterisks, with •p>0.05<0.1, *p<0.05, **p<0.01, ***p<0.001.
 4244

		<i>H. erythrogrmma</i> biomass	Turf	<i>E. radiata</i> recruits	<i>U. pinnatifida</i>	Survival (%)			<i>H. erythrogrmma</i> grazing rate		
Source	df	LRT	LRT	LRT		Source	df	LRT	Source	df	LRT
Kelp bed zone (KZ)	2	37.22***	101.54***	56.17***	84.02**	Kelp Stage (KS)	2	34.32**	Kelp Source (KS)	1	2.77
						Kelp bed zone (KZ)	2	8.24*	Kelp bed zone (KZ)	2	33.62***
						KS*KZ	4	11.09	KS*KZ	2	13.16**
Pairwise tests											
Kelp bed zone (KZ)		E>B>M	B=E>M	M>E>B	E>B>M	Kelp Stage (KS)	III>I, III=II, I=II		Kelp Source (KS)		-
						Kelp bed zone (KZ)	M>B=E		Kelp bed zone (KZ)		-
						KS*KZ			KS*KZ		Drift:B=E, B>M, E=M Attached:B>E, B>M, E=M

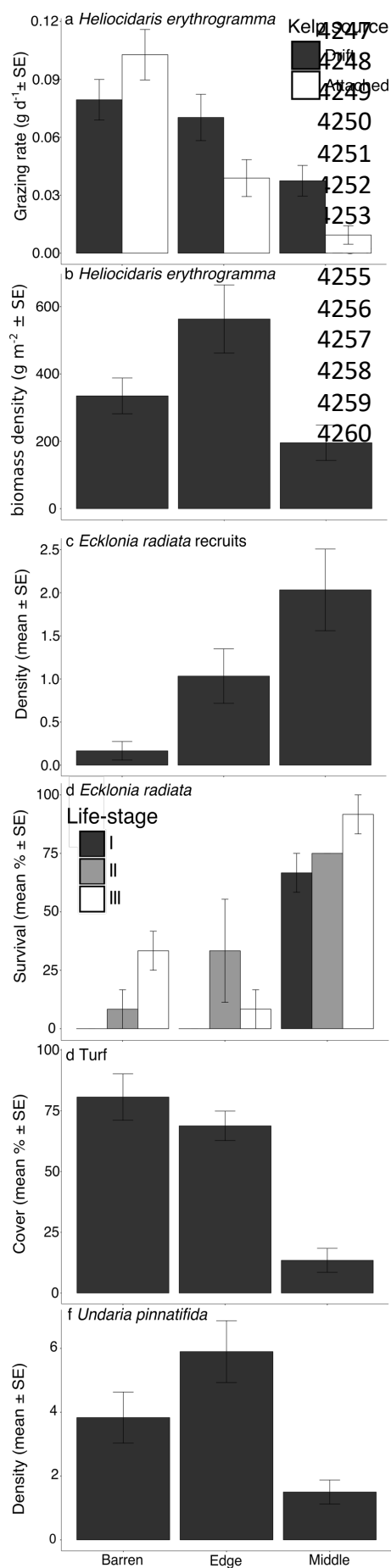


Figure 4. Dynamics of key processes, standing cover and biomass across Barren, Edge and Middle kelp bed zones. a) Mean *Heliocidaris erythrogramma* biomass density ($\text{g m}^{-2} \pm \text{SE}$, $n=30$); b) mean grazing rate ($\text{g d}^{-1} \pm \text{SE}$) of *H. erythrogramma* ($n=36$) on *Ecklonia radiata* 200 mm pieces deployed to mimic attached and drift kelp; c) mean *Ecklonia radiata* recruits per $\text{m}^2 (\pm \text{SE}, n=30)$; d) mean survival ($\% \pm \text{SE}, n=12$) of stage I, II and III *E. radiata* sporophytes; e) mean turf cover ($\% \pm \text{SE}, n=30$), and f) mean density of *Undaria pinnatifida* sporophytes per $\text{m}^2 (\pm \text{SE}, n=30)$.

Table 2. Results of PERMANOVA of a 2-way design testing kelp bed zones (3 levels - fixed: barren (B), edge (E) and middle (M)) and kelp bed (Bed - random) on substrate type percent cover. Degrees of freedom, Pseudo-F values. Significant effects are indicated by asterisks, with • $p > 0.05 < 0.1$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Results of a posteriori pair-wise tests for significant terms with SIMPER results describing the significant pair-wise tests are given in the lower section of the table.

Source	df	Pseudo-F	
Kelp-bed Zone (KZ)	2	0.67	
Bed (B)	2	<u>4.62***</u>	
KZxB	4	<u>2.49**</u>	
Error	81		
Pair-wise tests			
KZxB	Within Bed I: E≠B&M		
	Within Bed III: E≠M		
SIMPER for significant pair-wise tests			
Variable	Av Value (%)	Av Value (%)	Contribution (%)
	Bed I-Barren	Bed I-Edge	
Large boulder	22.8	73	43.32
Small boulder	61.8	26.5	36.58
	Bed I-Middle	Bed I-Edge	
Large boulder	32.8	73	43.6
Small boulder	67.3	26.5	43.37
	Bed III-Middle	Bed III-Edge	
Flat rock	35	10	23.98
Very large boulder	30	0	24.55
Small boulder	17.5	51.3	33.47

4273

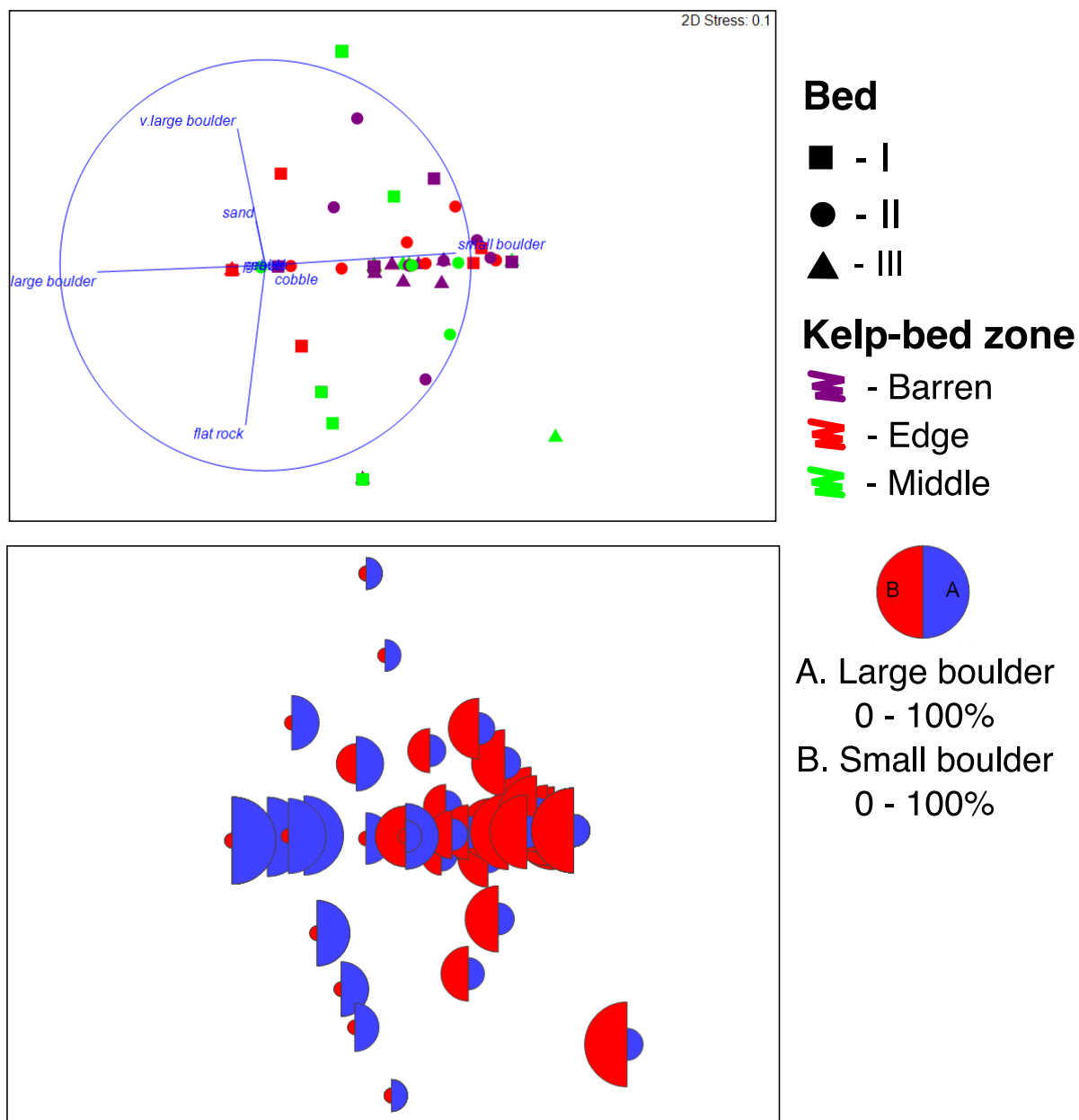


Figure 5. Non-metric multi-dimensional scaling (nMDS) plots exploring the Kelp-bed zone x Bed model of substrate type percent cover a) nMDS displaying the pattern of substrate type and a vector (Pearson correlation >0.05) plot showing the substrate types driving separation; b) displays a bubble nMDS for substrate type decomposed into large (>1 m and <2.5 m diameter) and small boulders (>0.2 m and <1 m diameter) substrate types (large boulders in position A – blue and small boulders in position B – red).

Discussion

Alongside individual kelp-loss and fragmentation of kelp beds, dynamic alterations in both bed size and shape occur. Sea urchin grazing pressure is the principal mechanism driving such dynamic alterations to kelp beds, with urchin biomass and grazing rates dually elevated in barren and edge zones of kelp beds. High urchin biomass in barrens results in overgrazing from the ‘outside-in’ and reduced survival of all kelp life-stages. When kelp is lost, competitive interactions with subordinate algal-guilds is reduced, leading to greater dominance by turfs and the invasive kelp *U. pinnatifida*. Increased competition for space and virtually zero likelihood of survival of newly settled kelp recruits, results in negligible recruitment of kelps into the barren and edge zones, effectively preventing recovery pathways and maintaining the unvegetated urchin barrens as an alternative and stable state (Filbee-Dexter and Scheibling 2014; Ling et al. 2015). Conversely, in the interior of patches where non-destructive sea urchin herbivory prevails, survival and recruitment of sporophytes are high and invasion by ephemerals low, and so the interior of kelp patches appears resilient to overgrazing. However, as kelp-loss occurs, the perimeter-to-area ratio of kelp beds increases, leading to greater intrusion of the edge zone into the resilient ‘heart’ of kelp beds, ultimately increasing the rate of kelp-loss.

Sea urchins as ultimate drivers of kelp-loss and turf development

In the current study, I observed that *H. erythrogramma* facilitates ecological change over Melbourne’s urban reefscape by exerting strong control over kelp beds (Fig. 1). Urchin biomass density in edge and barren zones of kelp beds at Williamstown was consistently higher than the urchin biomass ($\sim 427 \text{ g m}^{-2}$) estimated by Kriegisch et al. (2016) to be sufficient for complete overgrazing of kelp beds in northern PPB. The higher urchin biomass

in the edge zone ($563.2 \pm 101.24 \text{ g m}^{-2}$) is closer to the mean urchin biomass of $668 (\pm 115 \text{ g m}^{-2})$ that has been assessed as the threshold for which overgrazing is observed for rocky reef systems globally (Ling et al. 2015). The mean biomass of *H. erythrogramma* I observed in the interior of kelp beds ($195.68 \pm 101.24 \text{ g m}^{-2}$) is lower than the local threshold allowing macroalgal recovery post overgrazing at 213 g m^{-2} (Kriegisch et al. 2016). *H. erythrogramma* in the barren zones and edge zones of the kelp patches at Williamstown is at sufficiently high abundances to cause phase-shifts to urchin barrens, however, within the interior of kelp patches low urchin biomass provides a refuge for kelps from destructive grazing maintaining the kelp bed system.

At Williamstown, I observed a distinct shift in grazing behaviour of *H. erythrogramma* from the barrens and edge zones to that in the interior of the kelp beds, where grazing on attached algae was less important within the patch, and drift algae was the dominant food source. Several other studies have also reported this trend, where grazing pressure on attached kelp within kelp beds is low due to a ready supply of drift kelp (Kriegisch 2016, Dean et al. 1984, Harrold and Reed 1985). I suggest that there is a high supply of autochthonous drift kelp within the interior of kelp beds, which results in a 'sit-and-wait' (Higginson and Ruxton 2015) behaviour by *H. erythrogramma*, rather than active exposed-forging (Harrold and Reed 1985; Vanderklift and Kendrick 2005; Vanderklift and Wernberg 2008). This 'sit-and-wait' behaviour is thought to be an energy saving mechanism; as food supply becomes more readily abundant, individuals become increasingly sedentary to save energy and reduce the risk of predation (Higginson and Ruxton 2015; Parnell et al. 2017).

4331 The availability of physical refugia to urchins can also influence overgrazing. Physical refugia
4332 can be provided by increased topographical complexity and increases in structure results in a
4333 greater number of refuges available to urchins. Increased structure or the availability of
4334 crevices can influence overgrazing of kelp beds by providing refugia from predators (Andrew,
4335 1993; Benedetti-Cecchi and Cinelli, 1995; Spyksma et al. 2017) however, not all urchins are as
4336 dependent on refugia i.e. Diadematids (reliant) vs. Strongylocentrotids (less reliant) (Andrew,
4337 1993). Greatest structure can be provided by substrata ranging from substrate 2.0 – 0.2 m in
4338 diameter. Our observations suggest that *H. erythrogramma* in northern PPB are either less
4339 reliant on refuges provided by substrate or perhaps not driven to seek refugia due to the
4340 limited number of urchin predators in PPB.

4341

4342 An interesting finding from the current research was the observation of incipient
4343 barren formation within remnant kelp patches. This mode of overgrazing and barren
4344 formation, has been described by both Flukes et al. (2012) and Feehan et al. (2012), and
4345 manifests as the formation of discrete barren patches within a kelp bed, which grow in size
4346 and number with urchin density until they eventually coalesce to form widespread barrens
4347 habitat from the ‘inside out’. The appearance of these ‘incipient’ barrens patches provides
4348 quite a conundrum, as evidence suggests that drift kelp should suppress urchin overgrazing in
4349 the interior of kelp beds, but the incipient barren patches still occasionally occur. Further
4350 research is required to understand the factors that drive the appearance of these small-scale
4351 incipient barrens for *H. erythrogramma*, however, they are likely established from
4352 recruitment within the bed to suitable rocky crevices (e.g. Andrew 1993).

4353

Kelp-loss leads to proliferation of competitors and affects kelp recruitment

Survival of kelp sporophytes was strongly contingent on the zone in which they occurred and was negatively correlated with urchin biomass. Survival of all stages of *E. radiata* was minimal in the barren and edge zones but was most noticeable for the early recruits (Stage I's). Conversely, survival was greatest in the interior of kelp patches and explains the greater abundance of *E. radiata* recruits in that zone. The presence and density of adults influences settlement and early-stage survival of juvenile seaweeds through several different mechanisms. Both positive (i.e. stress amelioration Hurd (2000); Bennett and Wernberg (2014)) and negative effects of adults (i.e. interspecific competition or density-dependent effects (Irving et al. 2009; Capdevila et al. 2015)), on recruitment, have been described. *E. radiata* strongly influences its local environment by altering understory structure and mitigating the establishment of invasive macroalgae or dense turfs (Kennelly 1989; Irving et al. 2004; Irving and Connell 2006). This was evident in the current study, where turfs and the invasive *Undaria pinnatifida* were in high abundance when kelp cover decreased (e.g. in the Edge zone). Removal of the kelp canopy eliminates the negative effects of kelps on competitors (via increased light and decreased abrasion) that would otherwise limit the retention of space available to competitive subordinates (Connell 2003; Falkenberg et al. 2015).

Habitat edges are peculiar, often exhibiting the most suitable conditions for species survival (due to limited negative effects from adults), but also representing the first sites to be impacted by physical and biological disturbances (Konar and Estes 2003; Bulleri and Benedetti-Cecchi 2006). Both Kennelly (1987a) and Velimirov and Griffiths (1979) showed the importance of adult sporophytes on the edge of kelp beds as critical regions for the growth

and maintenance of the bed. Here sporophytes can help to maintain a predator/competitor free zone by the sweeping action of their fronds, and a single or small number of sporophytes can form a nucleus for a new kelp patch or help maintain an existing one. If several sporophytes survive nearby, they can sweep as a unit and act as a more substantial nucleus (Velmirov and Griffiths, 1979). However, loss of kelps due to urchin grazing results in double jeopardy for kelp resilience, as grazing removes adult kelps resulting in the loss of the provision of safe sites and propagule supply, but also ongoing urchin grazing results in poor or zero survival of kelp recruits, reinforcing a positive feedback through reduced drift supply to urchins. The added effect of competition from turfs, and nil survival of recruits in dense turf, shuts down the path to recovery of kelp patches. Thus, the edge of a kelp bed can be a site of both resilience for the kelp bed, but also the region affected most by sea urchin grazing.

The changing shape of kelp beds

By documenting the fragmentation of kelp bed patches in northern PPB, this study has identified three broad modes of kelp bed decline driven by sea urchin overgrazing (Fig. 6):

(I) Loss of kelp beds from the ‘outside in’ – or sea urchin grazing feeding-front (Scheibling and Anthony 2001; Lauzon-Guay and Scheibling 2007a; Lauzon-Guay and Scheibling 2007b; Feehan et al. 2012);

(II) Loss of kelp beds from the ‘inside out’ – formation of incipient patches as described above (Feehan et al. 2012; Flukes et al. 2012);

(III) Loss of kelp beds from a combination of both the ‘outside in’ & ‘inside out’ mechanisms.

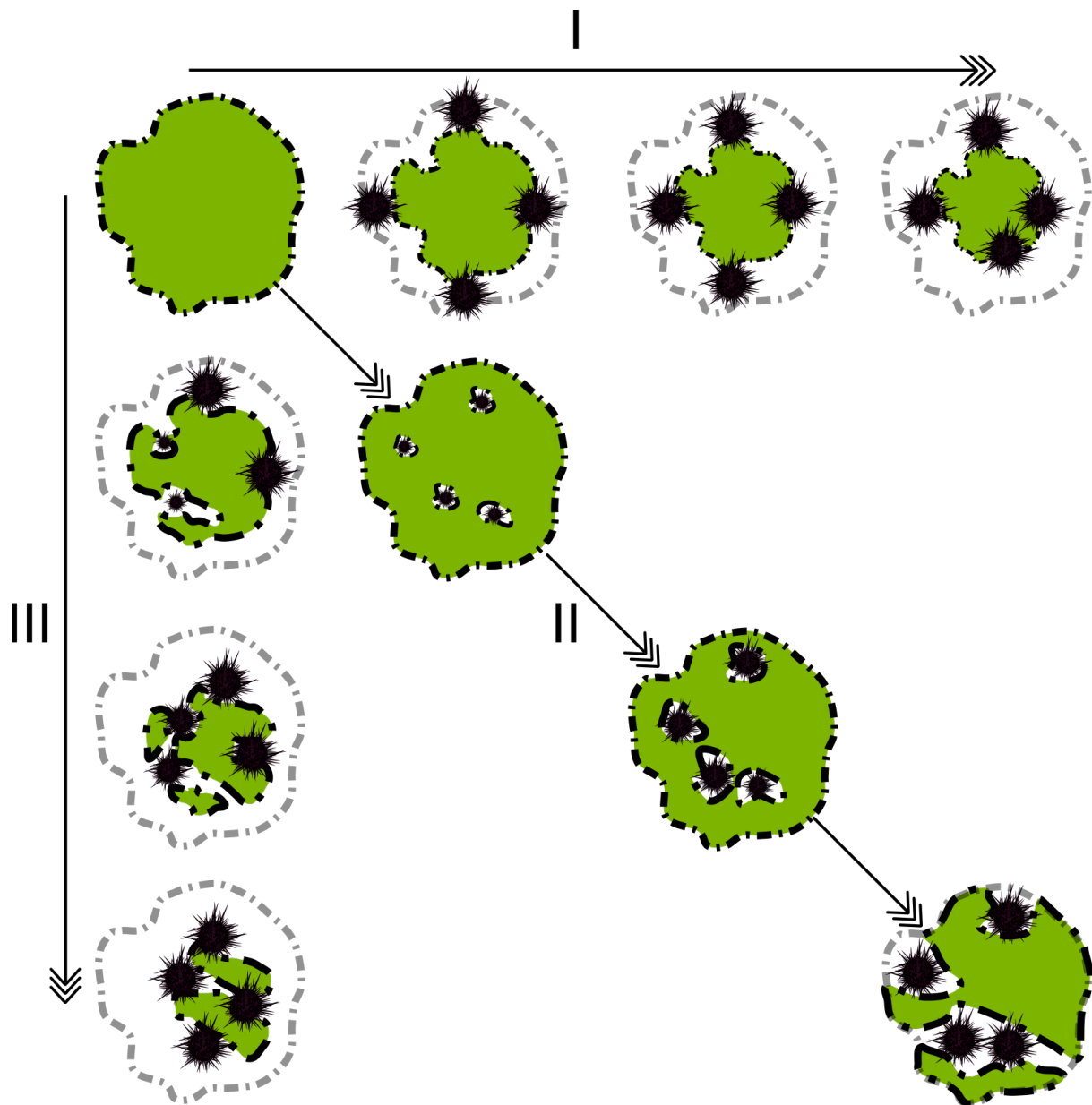


Figure 6. Conceptual diagram of modes of kelp bed decline driven by sea urchin overgrazing. Mode I describes loss of kelp beds from the 'outside in', akin to sea urchin on a front at the interface of the kelp patch and barren habitat (Scheibling and Anthony 2001; Lauzon-Guay and Scheibling 2007a; Lauzon-Guay and Scheibling 2007b). Mode II or loss of kelp beds from the 'inside out' to form incipient barren mechanism that manifests as an increased number of discrete incipient barren patches that grow by the recruitment and grazing activity of additional urchins, eventually coalescing to form widespread barrens from the 'inside out' (Feehan et al. 2012; Flukes et al. 2012). Mode III describes loss of kelp beds from a combination of modes I and II 'outside in' & 'inside out' simultaneously.

4415 This is the first time to our knowledge that such labile barren formation behaviours
 4416 have been reported in a single sea urchin species. Importantly, when mechanism 3 occurs,
 4417 kelp-loss appears accelerated due to the increased likelihood of fragmentation and rapid
 4418 increase in edge habitat. The shape of the kelp patch is a crucial determinant of kelp-loss
 4419 rate, with kelp-loss along long thin patch edges likely to be more rapid than along rounded
 4420 regular-shaped patches. As the shape of the kelp bed changes and bed fragmentation
 4421 increases so does the ratio of edge (perimeter) compared to the interior of the kelp bed
 4422 (area) (Fig. 3). As this ratio increases, the edge effects impacting on the resistant interior of
 4423 the kelp bed also increases, leading to reduced kelp cover and decreased ability to recover
 4424 post kelp-loss. Patches that have a high perimeter-to-area ratio will be less resilient and likely
 4425 persist for a shorter period than more regular and round shapes with low perimeter-to-area.

4426 *From individuals to seascapes - lessons for restoration*

4427 Structurally complex habitats are becoming rarer across temperate marine environments at
 4428 local, regional and global scales (Lotze et al. 2006; Airoidi et al. 2008; Krumhansl et al. 2016).
 4429 The present study has begun the process to comprehend the loss of structurally complex kelp
 4430 beds on the urban seascapes of Australia's fastest growing state capital city, the loss of
 4431 which, up until now, has largely only been recognised anecdotally (Jung et al., 2011),
 4432 however Carnell, 2014 described similar patterns of kelp loss for other location in PPB. Other
 4433 such studies have been undertaken for the metropolitan coastlines of Sydney (Coleman et al.
 4434 2008) and Adelaide (Connell et al. 2008) and have contributed to larger global studies (Ling et
 4435 al. 2015; Krumhansl et al. 2016). It is often the case that studies documenting declines of
 4436 important habitats are instrumental in building the case for subsequent restoration (Gillies et

4437 al. 2015). For example, the case of shellfish reefs (<http://www.natureaustralia.org.au/our->
4438 [work/oceans/restoring-shellfish-reefs/](http://www.natureaustralia.org.au/our-work/oceans/restoring-shellfish-reefs/))
4439 (Beck et al. 2011; Alleway and Connell 2015; Ford and Hamer 2016) and kelp populations
4440 (e.g. <http://www.operationcrayweed.com>) (Coleman et al. 2008; Campbell et al. 2014).
4441 Identifying decline is an integral part of the process of restoration; however, restoration
4442 cannot occur unless the proximate causes of these declines have been adequately identified
4443 (Johnson et al. 2017). This study has shown that to maintain and rehabilitate remnant kelp
4444 patches, sea urchins must be reduced and maintained at low numbers within the edge zone
4445 of the patches. Maintaining low urchin biomass will enhance survival of all kelp thalli around
4446 the edge of remnant kelp patches and increase clearance of turfing-algae promoting
4447 recruitment of juvenile kelps and overall persistence-stability of the bed, ensuring kelp bed
4448 edges act as zones of replenishment and growth not zones of destructive overgrazing and
4449 loss.

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4451

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4456

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CHAPTER 6: General discussion

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4744 In June 1802, Alexander Von Humboldt set out to climb what was then thought to be the
4745 world's highest mountain – Chimborazo in the Andes. At the height of 20,000 feet, looking
4746 down the slopes of the mountain at the patterning of vegetation and rock formations,
4747 Humboldt had an epiphany – of nature as a complex web of interactions between the
4748 physical, organic and human worlds. 'Humboldtian science' and thinking encouraged a
4749 generation of scientists, including Darwin, and deepened the environmental consciousness
4750 by inspiring writers such as John Muir and Henry David Thoreau. Even now, more than 200
4751 years on from Humboldt's ascent, understanding ecological interactions remains a critical
4752 focus of research efforts and lies at the heart of our ability to manage ecosystems and
4753 natural resources in the face of ongoing global change.

4754

4755 An ecological system is a network of various kinds of interspecific interactions, some
4756 positive and some negative, some stronger than others, with some so weak they appear
4757 close to neutral. Any event or phenomenon that alters the quasi-equilibrium in a web of
4758 interactions can facilitate a re-organisation in structure that could represent a wholesale
4759 change to the system (Holling 1973; Holling 1996; Folke et al. 2004). Ecological stability can
4760 be viewed as the ability of a system to cope with disturbances and stressors. Disturbances
4761 are defined as events/phenomena that remove biomass either total (mortality, dislodgement
4762 or forced emigration) or partial (erosion, grazing or predation) (Grime 1977; Chapman and
4763 Johnson 1990). Stressors are defined as external constraints which limit production such as
4764 resource limitation or environmental conditions at extremes of physiological tolerances
4765 (Grime 1977; Chapman and Johnson 1990) and include the possibility of community re-
4766 organisation to retain essentially the same function, but not necessarily the same
4767 complement of taxa (Folke et al. 2004). An ecologically stable system is thought to be i)

4768 resistant – having the capacity to withstand a disturbance/stressor, and ii) resilient – having
 4769 the capacity to recover from a disturbance/stressor that causes a change in community
 4770 structure, usually through species losses resulting in shifts in relative abundance (Connell and
 4771 Sousa 1983; Pimm 1984; Tilman and Downing 1996; Lake 2013; Nimmo et al. 2015).

4772 For many temperate reef systems, canopy-forming macroalgae are foundation
 4773 species, as they have a disproportionate influence on the structure of these communities
 4774 (Dayton 1972). This thesis has demonstrated how modifications to four processes can result
 4775 in considerable alteration to reef communities: 1) depletion or 2) increase of a foundation
 4776 species, 3) addition of non-native species, and 4) the addition and interaction of multiple
 4777 direct human-stressors. The key findings of this thesis can be generalised within a qualitative
 4778 model defining the interactions between principal biological components and underlying
 4779 processes of rocky reefs in Port Phillip Bay, illustrating how the above four events influence
 4780 these interactions and propagate change throughout the system (Fig. 1). This model
 4781 encapsulates the complexity of the interactions that drive kelp bed structure and function,
 4782 including the strong interactions associated with the kelp *Ecklonia radiata*, the critical
 4783 positive feedbacks in kelp dynamics throughout its lifecycle, and the overwhelming adverse
 4784 effect of grazing by the sea urchin *Heliocidaris erythrogramma*.

4785 The ability of formerly dominant species to recover from disturbance through natural
 4786 recruitment is an essential process for ecosystem stability and determines landscape
 4787 dynamics of ecosystems (Fig. 1), especially for foundation or ecosystem engineering species.
 4788 For many primitive autotrophs such as kelps (here including large brown algae in the order
 4789 Laminariales and Fucoidea – Dayton 1985, Steneck and Johnson 2013, Schiel 2006), the
 4790 process of recruitment (i.e., the first appearance of macroscopic individuals) is complex and

4791 requires the successful completion of a microscopic free-living sexual stage see Fig. 1 –
 4792 Chapter 1 (Reed 1990a; Schiel and Foster 2006).

4793

4794 Kelp for kelp's sake

4795 Across all life-stages of the kelp *Ecklonia radiata*, there appear to be positive feedbacks
 4796 where the presence of one or more kelp sporophytes increases the recruitment, fitness, and
 4797 survival of others (Fig. 1). For *E. radiata*, as with other organisms that participate in group
 4798 living strategies (e.g. shoaling fish and colonies of sessile invertebrates), there are
 4799 considerable benefits of conspecific associations, including reduced predation, increased
 4800 reproductive success and amelioration of physical stress, which likely outweighs the costs of
 4801 intraspecific competition. Chapter 2 showed how larger densities of *E. radiata* sporophytes
 4802 results in greater supply of spores enhancing propagule pressure (Fig. 1). High propagule
 4803 pressure is important as an optimal minimal density of $> 10^6 \text{ m}^{-2}$ (1 spore mm^{-2}) is required
 4804 for successful recruitment of many macroalgal species (e.g. *Macrocystis pyrifera* and
 4805 *Pterogophora californica* (Reed et al., 1990)). This minimum spore and gametophyte density
 4806 is defined in part by the maximum distance that male and female gametophytes can be
 4807 separated while still allowing fertilisation to occur. Fertilization in true kelps (Order
 4808 Laminariales) is enhanced by a pheromone emitted from the egg that triggers both the
 4809 release and attraction of sperm from the male gametophyte (Lüning and Müller 1978; Müller
 4810 et al. 1985; Maier and Muller 1986). Laboratory studies indicate that the range of attraction
 4811 of an egg emitting the pheromone does not exceed 1 mm (Müller 1981) Therefore, increased
 4812 production of zoospores will increase the likelihood of settlement at sufficient densities to

4813 maximise the likelihood of successful fertilisation. Any abiotic process that limits the density
4814 of propagules may thus drastically decrease successful settlement and fertilisation of kelps.

4815

4816 *Low and slow – the importance of physical refugia*

4817 Marine algae growing at higher densities experience less water motion and decreased
4818 velocities than those at lower densities (Choat and Schiel 1982). Physical refuge from water
4819 motion is crucial for early life-stages of kelps (Bennett and Wernberg 2014) and promotes the
4820 recruitment of more kelps (Fig. 1). In Chapter 2, increased sediment deposition in kelps beds
4821 was identified relative to areas devoid of kelps (i.e. urchin barrens). This accumulation of
4822 particulates on the benthos is related to the reduction in mass transport and shear beneath
4823 kelp canopies (Eckman et al. 1989; Duggins et al. 1990, Graham, 2003). These findings
4824 suggested that kelps retard the transport of particles contained beneath the canopy and.
4825 Consequently, dispersal distances of short-lived planktonic larvae or zoospores may be more
4826 limited beneath kelp canopies than on more exposed bottoms subjected to stronger currents
4827 (Duggins et al. 1990, Graham, 2003). Lowered water velocity would positively impact
4828 settlement of zoospores and fertilisation during the gametophyte stage, as lowered water
4829 velocities are likely to decrease the advection of propagules (sperm and zoospores) away
4830 from a kelp bed. Advected propagules would influence recruitment in two ways: 1) advected
4831 zoospores have a higher risk of settling away from a kelp bed in areas sub-optimal for
4832 recruitment, for example in areas with high cover of interspecific competitors (i.e. turfs), or
4833 where densities of gametophytes are too low for successful fertilisation, and 2) lowered
4834 water velocities within kelp beds will not only increase residence time of pheromones
4835 produced by the female gametophyte (crucial for triggering release of sperm) but also
4836 increase residence time and decrease dilution of the released sperm, increasing the

4837 likelihood of successful fertilisation. Furthermore, following fertilisation, juveniles and
4838 germlings will develop in the benthic boundary layer (BBL), provided by adult kelps. Thus,
4839 early recruits will experience reduced shear stress from elevated water velocities compared
4840 to macroalgae whose canopies extend beyond the BBL (Hurd 2000). While also providing
4841 refugia for early recruited kelps, the BBL also acts to mitigate the impact of flow for algae
4842 (such as turfs) that may increase interspecific competition on early kelp life-stages.

4843

4844 Physical refugia can also be provided by increased topographical complexity and more
4845 refuges can influence both urchins and algae. Increased structure or the availability of
4846 crevices can influence overgrazing of kelp beds by providing refugia from predators (Andrew,
4847 1993; Benedetti-Cecchi and Cinelli, 1995; Spyksma et al. 2017) however, not all urchins are as
4848 dependent on refugia i.e. Diadematids (reliant) vs. Strongylocentrotids (less reliant) (Andrew,
4849 1993). Additionally, topographical refugia can influence the likelihood of grazing upon kelp
4850 recruits, as kelps (adults and recruits), like urchins, can survive better in crevices and gaps
4851 provided by topographical heterogeneity, particularly under high consumptive pressure
4852 (Franco et al. 2015). However, this will be influenced by the guild of grazer, as topographical
4853 refugia could play a far greater role when grazing fish are more abundant than urchins, as
4854 urchins may be more likely to overgraze the majority of the substrata (including crevices)
4855 compared to fish. Therefore, the identity of the grazer will influence the importance of
4856 topographic refugia for kelp recruits.

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Kelp laminae sweeping the seafloor – creating spatial refugia

The success of kelp propagules varies spatially and temporally across the dispersing environment. Variability leads to patchiness across reefscapes, which can be viewed as a patchwork mosaic of available habitat (Levin and Paine 1974; Green 1983; Reed 1990a; Reed 1990b). These patches vary in age, size, and other factors that influence their suitability for any given species (Green 1983). ‘Safe sites’ (*sensu* Harper, 1965) define suitable patches that support the safe development of a species’ propagules (Green 1983). Safe sites for the recruitment of kelp are spatially and temporally variable, and are likely strongly related to density-dependent effects from adult conspecifics, since adult kelps can have both strong positive and negative effects on settlement and early-stage survival of juvenile seaweeds through various mechanisms (Fig. 1).

4871

Chapters 2, 3 and 4 showed that like many other kelp species, *Ecklonia radiata* exerts a strong structuring effect on the benthos, as adult *E. radiata* sporophytes efficiently out-compete turfs (Fig. 1), invasive species, and native understory taxa, while also benefitting some taxa that are weak competitors (i.e. encrusting coralline algae). Adverse effects of abrasion of the seafloor (chapter 3) and shading by laminae of adult *E. radiata* on understory taxa maintain extensive cover of non-geniculate encrusting coralline algae beneath the canopy (Irving et al. 2004; Irving and Connell 2006), which provides a stable substratum essential for *E. radiata* Stage I settlement and recruitment to reproductive stages (Fig. 1 and Chapter 3). Conversely, the removal of the adult kelps eliminates the effects of abrasion and shading on understory taxa, resulting in uptake of space by subordinate algal species, thus reducing available safe sites for early life-stages of kelp. Furthermore, there is an additive effect from the loss of kelps and the addition of nutrients (Chapter 4). Nutrification

4884 compounds the impact of losing kelp, as available substrata feed by disturbance is more likely
 4885 to be dominated by turfing species that inhibit kelp recruitment. Thus, despite negative
 4886 effects from intraspecific competition between adult *E. radiata* and early recruits (Fig. 1),
 4887 kelps provide a critical function in creating refugia and maintaining safe sites for kelp
 4888 recruitment.

4889

4890 ***Altruistic suicide – creating trophic refugia***

4891 Most of the primary production of kelp ecosystems flows through detrital pathways
 4892 (Krumhansl and Scheibling 2012). Kelp detritus ranges in size from small particles to whole
 4893 thalli. Small particles are produced from the distal tips of blades eroding, larger amounts of
 4894 biomass loss occur when whole sporophytes become dislodged, or blades break off. Detrital
 4895 kelp can settle within kelp beds and can also be exported to nearby and distant ecosystems,
 4896 including sandy beaches, rocky intertidal shores, rocky and sedimentary subtidal areas, and
 4897 the deep sea (Bishop et al. 2010; Krumhansl and Scheibling 2012; Tait et al. 2015; Suárez-
 4898 Jiménez et al. 2017). Exported kelp detritus can provide a significant resource subsidy and
 4899 enhance secondary production in these communities. (Bustamante and Branch 1996; Bishop
 4900 et al. 2010 Krumhansl and Scheibling 2012). Chapter 2 showed that a considerable amount of
 4901 the annual biomass produced by *E. radiata* is eroded and this may provide a significant
 4902 trophic subsidy to nearby areas of low productivity. Similar processes have been shown to be
 4903 the case in Nova-Scotia (Krumhansl and Scheibling 2011), California (Dean et al. 1984;
 4904 Harrold and Reed 1985) and Western Australia (Vanderklift and Kendrick 2005; Wernberg et
 4905 al. 2006; Vanderklift and Wernberg 2008). In some instances, this detrital subsidy, or loss
 4906 thereof, has been linked to switches to destructive over-grazing of attached kelps (Dayton et
 4907 al. 1984; Harrold and Reed 1985; Lauzon-Guay and Scheibling 2007a; Kriegisch et al. 2016).

Chapters 2 and 5 showed how grazing by *Heliocidaris erythrogramma* is a fundamental driver of *E. radiata* mortality, particularly of recruits (Stage I). In Chapter 5, when a consistent supply of kelp in the form of drift was available (i.e. in the interior of patches), urchins were shown to predominantly graze on this drift source as opposed to exhibiting destructive forms of herbivory on attached kelps (as is evident in barrens and edge zones of kelp beds). Where drift consumption is predominant, survival of all stages of *E. radiata* increases from 0 to 75-100%, and this is particularly evident for newly recruited individuals. Low detrital supply, therefore, triggers the transition from a highly productive resistant and resilient kelp bed, to a low-productivity sea urchin barren (Fig. 1). Thus, adult kelps provide a refuge from herbivory through the provision of this trophic subsidy via removed and drifting kelp pieces (Krumhansl and Scheibling 2012).

All these factors explored throughout this thesis are examples of how kelp ‘begets kelp’, and these convey both resistance and resilience to kelp beds. This thesis has shown that if kelp is not present, then a wholesale shift occurs on PPB reefs towards a state dominated by foliose algae and turfs that in turn greatly reduce kelp recruitment. Therefore, effective management is required that will conserve or restore kelp beds. Current kelp biomass appears insufficient to maintain essential functioning; thus, to maintain a viable connected network of kelp beds, management efforts must focus on the drivers of kelp losses and active management is required to restore them.

Urchins as a key driver of loss

Grazing by herbivores is frequently implicated as a key driver of phase shifts in marine environments through the removal of primary producers and biogenic habitat. Chapters 2

through 5 of this thesis have shown that on shallow temperate reefs in PPB, sea urchins are a dominant habitat-structuring taxon, given their capacity for intensive grazing, which triggers a shift from dense macroalgal beds to ‘barrens’ habitat largely devoid of fleshy macroalgae (Lawrence 1975; Ling et al. 2015). It was not an initial aim of this thesis to investigate the impacts of urchins on kelp, but urchins are a critical component of this temperate reef system and their impacts infiltrated every question and experiment of this thesis. In comparison to the other urban stressors tested in chapters 3 and 4 (sedimentation, nutrients), the effects of urchins overwhelmed them all. Chapter 2 shows how urchins directly impact kelp beds; as urchin densities increase, kelp cover decreases. However, this research has also shown that the interactions between urchins and kelp can be expressed in more complex ways than this.

Urchins as drivers of the reefscape and local species pools

H. erythrogramma grazing significantly alters the reefscape in PPB by removing kelps (Fig. 1), driving change in community structure resulting in increased turf cover (Chapters 2, 3 and 4; Fig. 1), which in turn limits recruitment of kelps and slows kelp recovery. *H. erythrogramma* barrens have a somewhat different nature to other urchin-barrens formed by other species of sea urchins in Australia (Ling et al. 2010). For example, *Centrostephanus rodgersii* barrens are predominantly devoid of all erect algae and dominated solely by bleached coralline cover (Ling 2008). In contrast, *H. erythrogramma* barrens are often not wholly devoid of algae (Johnson et al. 2004; Valentine and Johnson 2005b; Valentine and Johnson 2005a). In PPB, *H. erythrogramma* barrens are typified by opportunistic species i.e. turfs (Chapters 2, 3, 4 and 5). This could result from high nutrient loading in PPB, leading to proliferation of opportunistic species following clearance of kelps by urchins. Alternatively, this pattern could

4955 be due to the different feeding behaviour of *H. erythrogramma* compared to other barren
 4956 forming urchins. *C. rodgersii* shows different behaviour patterns to *H. erythrogramma*,
 4957 particularly in showing little chemosensory attraction to kelps (Flukes et al. 2012), unlike *H.*
 4958 *erythrogramma* and other urchin species (Burdett-Coutts and Metaxas 2004; Wright et al.
 4959 2005; Feehan et al. 2012). Additionally, *C. rodgersii* shows strong homing to available
 4960 crevices, rarely moving greater than 2 metres away from a crevice (Flukes et al. 2012),
 4961 whereas *H. erythrogramma* seem less attached to refuges, especially when resources are
 4962 low, and show a propensity for mobile foraging. The distinct grazing behaviours of *H.*
 4963 *erythrogramma* has implications for resilience of kelp beds following urchin overgrazing
 4964 because the local algal species pools of *H. erythrogramma* barrens in PPB are dominated by
 4965 early successional species (turfs and filamentous algae) (Chapter 3 and 4) that subjugate all
 4966 available safe sites for kelp. Indeed, without established adult sporophytes to provide the
 4967 spore supply, physical, spatial and trophic refugia required for successful recruitment, the
 4968 likelihood of a kelp propagule finding a safe site within *H. erythrogramma* barrens is
 4969 negligible, resulting in an impasse for resilience of individual thalli and ultimately entire kelp
 4970 beds in PPB.

4971

4972 ***The importance of grazing behaviour***

4973 The grazing behaviour of urchins in PPB, even at a single site is relatively labile, with urchins
 4974 in kelp beds at low densities having little effect, whilst aggregated urchins, even small
 4975 distances away, graze destructively. In Chapter 5, I showed that even over a distance of ~5
 4976 meters across the ecotone at the edge of a kelp bed, urchin densities vary greatly and that
 4977 these urchins exhibit very different behaviours. Urchins in the barrens are exposed and more
 4978 likely to be actively foraging. Urchins in the edge zone show tendencies towards destructive

4979 aggregated feeding on kelps, whereas urchins in the interior of a kelp bed exhibited cryptic
4980 non-destructive grazing behaviour and feed on drift material. Supply of drifting kelp pieces in
4981 several other systems is important (Harrold and Reed 1985; Lauzon-Guay and Scheibling
4982 2007a; Lauzon-Guay and Scheibling 2007b) and the loss of drift kelp is apparently key to
4983 triggering destructive grazing. Greater densities of urchins in barrens, and potentially some
4984 attraction to remnant kelp, drives the formation of feeding fronts at the edge of kelp beds,
4985 where greater numbers of urchins graze on attached kelps (Lauzon-Guay and Scheibling
4986 2007b; Feehan et al. 2012). Chapters 3 and 5 showed that urchin density is correlated with
4987 the extent of destructive grazing, impacting both survivorship and cover of kelps. Higher
4988 densities of urchins drive local kelp cover lower than in areas with lower densities of urchins,
4989 which results in a greater likelihood of further destructive grazing. Moreover, as urchin
4990 densities increase and kelp is increasingly lost to overgrazing, the supply of drift kelp also
4991 decreases, creating a positive feedback loop that further accelerates kelp loss (Chapter 5).

4992

4993 Destructive grazing by urchins alters both the cover of kelp and the size and shape of
4994 kelp patches, leading to accelerated kelp loss (Chapter 5). Feeding-front aggregations at the
4995 edge of patches are more destructive than passive feeding, which occurs within the interior
4996 of the kelp bed, therefore as kelp patch size is reduced by grazing, kelp loss escalates. The
4997 behaviour of urchins and creation of urchin barrens is an important mechanism for
4998 fragmentation and loss of kelp beds. The interaction between kelp bed shape and size and
4999 urchin behaviour was a key determinant of the persistence of kelp beds (Chapter 5). Urchins
5000 aggregated in the ecotone between urchin barrens and kelp beds forming feeding-fronts,
5001 often resulting in multiple urchins aggregating on a single kelp sporophyte. This mode of
5002 barren-formation caused loss of kelp bed habitat from the outside-in. Additionally, a second

mode of barren formation resulted in kelp loss from the inside-out, as incipient barrens form in the interior of kelp beds. However, greatest kelp loss and likelihood of fragmentation was observed when both barren formation mechanisms occurred in concert. When both ‘outside-in’ and ‘inside-out’ modes co-occur, this is more likely to result in irregular shaped kelp beds, and irregular shapes result in the creation of more edge habitat, relative to the interior area of kelp beds. As the edge effect increases, more kelp sporophytes are exposed to urchins attracted in from the barrens, enhancing the capacity for destructive overgrazing.

5010

The interaction between urchin grazing and anthropogenic stressors, specifically elevated nutrients, also appears to contribute to enhanced kelp loss. Chapter 4 showed that enhanced kelp loss occurred on plots enriched by nutrients and this was explained by elevated urchin biomass on these plots, suggesting increased grazing pressure (Fig. 1). This implies that kelps may become more ‘attractive’ to urchins if nutrients are enhanced, potentially altering the C:N and C:P ratios of the algae. Grazers often increase consumption of nutrient-enriched algae (Lotze et al. 2000; Bokn et al. 2003; Ghedini et al. 2015) as C:N and C:P ratios increase, making algae more palatable and nutritionally appealing (Bokn et al. 2003; Hay et al. 2011). The increased consumption suggests that kelps growing along urbanised coastlines could be more appealing to urchins due to their exposure to higher elevated nutrients, leading to more destructive overgrazing in these regions. Other recent studies have indicated that resistance to compounding disturbances (i.e. local canopy-loss, eutrophication, ocean acidification) can be improved due to enhanced trophic control of turfs by grazers (Connell and Ghedini 2015; Ghedini et al. 2015). This thesis, however, suggests that this could be highly context-specific, dependent on location and the type of grazer, and this observation is supported by broad reviews on herbivore impacts (Poore et

al., 2012). I observed very little evidence of any trophic compensation from alternative algal sources to grazers in PPB. This could be due to preferential grazing of kelps over turfs (Wright et al. 2005; Poore et al. 2012), which results in a trophic refuge for turfs from urchin grazing and an indirect positive feedback to turf from urchins. Additionally, Chapter 4 showed that different kelp types might be more attractive to urchins, as urchins graze preferentially on *E. radiata* over fucoids. This could be driven by varying degrees of palatability associated with phlorotannin levels and the nutritional value of different algae determined by C:N and C:P ratios (Steinberg 1984; Steinberg 1989; Yates and Peckol 1993; McShane et al. 1994), that could contribute to selective grazing by urchins. Nevertheless, selective grazing of kelps over turfs results in shifts from kelp beds to urchin barrens with local species pools dominated by turfs. The dominance of turfs on urchin barrens in PPB suggests that shifts back to kelp beds are unlikely, even if urchin biomass is reduced back to levels necessary to promote kelp bed recovery (i.e. less than ≤ 4 urchins m^{-2} or ≤ 213 g m^{-2}) Kriegisch et al., 2016). This lack of kelp bed recovery occurs as no kelps remain to provide spores and physically disturb the turf to provide the safe sites necessary for kelp recruitment (Fig. 1)

Urchins have long been known to drive loss of structurally complex kelp bed habitats. This thesis emphasises that urchins are the dominant driver of kelp loss in PPB even though this heavily urbanised system received high levels of anthropogenic eutrophication. Kelp beds that are already in ‘trouble’ (i.e. fragmented patches within the urbanised environment) are the most vulnerable to ongoing destructive grazing. Furthermore, once urchin barrens are formed, the likelihood of shifts back to a kelp bed community is low due to the predominance of opportunistic species in depauperate local species pools that limit kelp recruitment when they form dense turfs, thus slowing or potentially halting kelp recovery in

the urbanised environment (Fig. 1). Management action (culling or fishing of urchins) to reduce urchin biomass density to below the urchin-barren kelp bed tipping point (Kriegisch 2016), is essential and can play a significant role in building ecological resilience of kelp beds (Kriegisch et al. 2016). In other locations implementation of Marine Protected Areas (MPA) have strengthened top down control of urchins via trophic cascades by prohibiting fishing of urchin predators (Lobsters – *Jasus* spp. and large predatory fish >300mm fork length) and has resulted in recovery of urchin barrens back to kelp beds (Babcock et al. 2010). However, in PPB where urchin predators have long since declined and are largely absent (Jung et al. 2011) passive approaches for kelp restoration are not appropriate with large urchin barrens growing in size in many MPAs in PPB (Constable, 1990; Carnell, 2014). Therefore, active restoration approaches are perhaps more appropriate. These active approaches could target removals of urchins around troubled or significant kelp beds (i.e. those vital for maintaining connectivity) and would significantly contribute to maintaining ecological stability of kelp ecosystems.

Canopy lost

Factors impacting the capacity for kelp beds to recover and maintain a particular community configuration post perturbation are complex. These processes are influenced by a multitude of extrinsic and intrinsic factors (Conversi et al. 2015), such as the source and regime of the perturbation, environmental (e.g. nutrients and space) and biological (e.g. predatory pressure or availability of food) drivers, and adaptive, competitive, and reproductive characteristics of the space occupiers (Grime 1977; Paine 1984; Airoldi 1998). Chapters 1-4 of this thesis showed that in all but a small number of occasions, removal of kelp ultimately

resulted in a reef community dominated by the turf-sediment matrix, filamentous algal or, depending on seasonal timing, *Undaria pinnatifida* dominated reef community with an absence of native canopy-forming kelp or fucoid algae. An increasing number of studies globally now show that recruitment of kelp is negatively correlated with recruitment and abundance of species of filamentous brown and algae (Reed 1990a; Valentine and Johnson 2003; Connell et al. 2008; Gorman and Connell 2009; Strain et al. 2014). Both kelp and/or turfing algae can inhibit the recruitment of kelps. However, removal of turfing species does not necessarily result in kelp recruitment, as outlined in Chapter 3. Kennelly (1987) showed turf inhibited kelp recruitment, even during dense recruitment periods in spring, and persisted for up to 2 years, until kelps encroached into clearings from the edges.

Reef systems that have shifted to turf or urchin barrens that are >100 m from a kelp bed represent a particular challenge for managers. This challenge is in part due to the life-history of kelps, which imposes significant constraints on their ability to colonise distant sites (Dayton 1985). As previously discussed, the two-stage life history of kelps requires high densities of spores to settle because male and female gametophytes need to settle close to one another for successful colonisation (Schiel and Foster 2006). As the dispersal distance gets larger, the likelihood of male and female spores settling close to one another becomes less (Kinlan et al. 2005). Furthermore, the likelihood of safe sites for kelp recruitment is reduced further away from the physical and spatial refugia provided by kelp sporophytes. Safe-sites are further reduced in turf and urchin barrens due to high interspecific competition and grazing pressure. Therefore, transplanting mature adult kelp sporophytes in parallel with reductions in urchin biomass (below the threshold kelp-barren tipping point) would be the best approach to shift turf and urchin barren systems back to kelp beds. Transplantation will

not only guarantee spore supply, but the sweeping protection will provide the physical and spatial refugia required for successful kelp recruitment. The nucleus of transplanted kelps can then act as a founder population instigating the expansion and resilience of kelp beds, though more work is needed to determine the size of a founder population that can be self-sustaining (Fig. 1).

5103

5104 **Apparent importance of algal diversity for kelp bed resilience**

The role of biodiversity in ecosystem functioning has been debated, and the consensus suggests that species diversity contributes to resilience (Elmqvist et al. 2003; Nyström 2006). However, its role in ecosystem functioning is still highly contested (Hoey and Bellwood 2011). Chapter 4 revealed site-specific differences in responses to multiple stressors, and large differences in diversity of the algal communities appeared to provide important context for this result. For example, at the northern site, an additive response from canopy-removal and nutrients was observed, which resulted in a shift to a turf-dominated community, whereas this additive effect did not occur in the southeast. In the north, the kelp beds were monospecific beds of *E. radiata*, where the strong negative interactions (abrasion and shading) with the underlying community results in a low diversity, structurally simple, understory community comprised of encrusting coralline algae. A similar pattern has been reported across southern Australia (Fowler-Walker and Connell 2002; Goodsell and Connell 2002). However, if urchin grazing or other disturbance removes the canopy, all that remains to compete for space is ECA, which is either competitively subordinate (Breitburg 1984; Bulleri 2006) or tolerant to overgrowth by foliose and turfing taxa (Kendrick 1991; Airolidi 2000; Bulleri 2006). Nevertheless, the outcome is that, with no other foliose algae to

compete with turfs for space, the turfs become dominant and maintain occupancy of space through positive feedbacks. In southeast PPB, *E. radiata* does not dominate, and the canopy-forming guild is more diverse, comprising of *E. radiata* and up to 6 – 7 Fucales species. The adverse effects of this mixed canopy-forming guild on the underlying algal community were not as strong, which resulted in a rich and diverse understory community. The diversity of understory in the southeast of PPB appeared to be positively affected by elevated sedimentation by enhancing richness. Thus, once canopy-formers are removed, there remain many species that compete for space with turfs and other ephemerals, providing enhanced resistance to shifts to alternative turf states. Additionally, unlike laminarians, fucalian taxa can regenerate from remnant holdfasts that remain following loss of the thallus, which tends to decrease spatial and temporal variability in adult density (Kendrick and Walker 1994; Schiel and Foster 2006). The fucoid-dominated seaweed bed suggests potential emergence of a novel resistant and resilient assemblage under urban regimes (Fig. 1). Whether resistance and resilience properties of the fucoid canopy under an urbanised environment reflects fucoid biological characteristics (i.e. capacity to re-grow from small amounts of remaining biomass, recruit into turf dominated areas and un-palatability to sea urchins) or is related to diversity of the macroalgal community, or both, is uncertain.

According to the insurance hypothesis of biodiversity, resistance and resilience should increase with species richness, because a greater number of species can express a greater range of responses to environmental perturbations (Pfisterer and Schmid 2002). Results from Chapter 4 provide support for ecosystem stability being supported by diversity. As such, a diverse group of species delivers a web of interactions that spread both the risks and benefits of stressors widely, retaining assemblage structure and function independent of wide

5145 fluctuations in individual species (Peterson et al. 1998; Gunderson 2000; Elmqvist et al.
 5146 2003). Chapter 4 suggests that high diversity, particularly under multiple stressors, reduces
 5147 canopy loss of established kelp bed assemblages – correlates with enhanced resistance – and
 5148 canopy resilience. Indeed, these relationships hold even when subject to multiple stress
 5149 scenarios, suggesting species diversity will become increasingly important under threats
 5150 imposed by multiple interacting anthropogenic stressors. Thus, conservation efforts that
 5151 focus on maintaining diverse functional groups of algae may provide a more effective
 5152 approach to restoration by monoculture of *E. radiata*.

5153 Conclusions

5154 This thesis has made a significant contribution towards furthering our mechanistic
 5155 understanding of the processes that reinforce or overwhelm stability of kelp bed systems.
 5156 The suite of field experiments and surveys defining this thesis span multiple-spatial scales
 5157 (from sub-metre to 1000s of metres), include multiple stressors associated with urbanisation
 5158 and considers multiple life-history stages of kelps. This approach has led to a comprehensive
 5159 understanding of processes affecting the cover of kelps, turfs and fucoids, and ultimately has
 5160 highlighted management actions available to minimise loss and maximise the resilience of
 5161 kelp beds under highly urbanised regimes. This thesis confirms the importance of kelps for
 5162 maintaining strong interactions resulting in a system that is both resistant and resilient.
 5163 However, throughout this study kelp beds were still being lost, fundamentally driven by high
 5164 densities of the sea urchin *H. erythrogramma*. The interaction between direct anthropogenic
 5165 stressors, in particular, elevated nutrients, and loss of kelps via urchin grazing, shifted this
 5166 reef system to a state dominated by opportunistic turfs that are also maintained by positive
 5167 feedbacks, which may ultimately create reef conditions unfavourable for kelp resilience. The

findings discussed by this thesis can be synthesised into six conclusions relevant to management and functional restoration of kelp beds:

1. Reducing urchin-driven disturbance to kelps beds can safeguard against kelp losses from the direct or indirect effects from sediments and/or nutrients;
2. Targeted control of urchin biomass (via fishing or culling) can yield significant benefits to existing and restored kelp beds;
3. Transplantation of adult sporophytes to areas devoid of kelp can represents a viable method of kelp bed restoration, particularly when combined with (2);
4. Management efforts could focus on maintaining existing kelp beds as more effort is required to recover kelp beds when lost, than to maintain when present;
5. Restoration or conservation efforts (where appropriate) could focus on maintaining/restoring diverse functional groups within the algal community to contribute to rich local species pools as opposed to focussing on recovering simplified communities such as the *Ecklonia radiata* – encrusting coralline complex;
6. Greater appreciation of processes at the reefscape scale i.e. minimising fragmentation and edge-to-perimeter ratio of kelp beds can promote resilience and resistance that can302 ‘buy time’ to achieve 1-5 above.

These actions represent mechanisms that should not be thought of independently but should be implemented in concert. In doing so, we as a community (scientists, managers, citizen scientist, fishers etc.) may be able to halt the further collapse of kelp beds, ensuring the continued provision of benefits for humans and nature for many years to come.

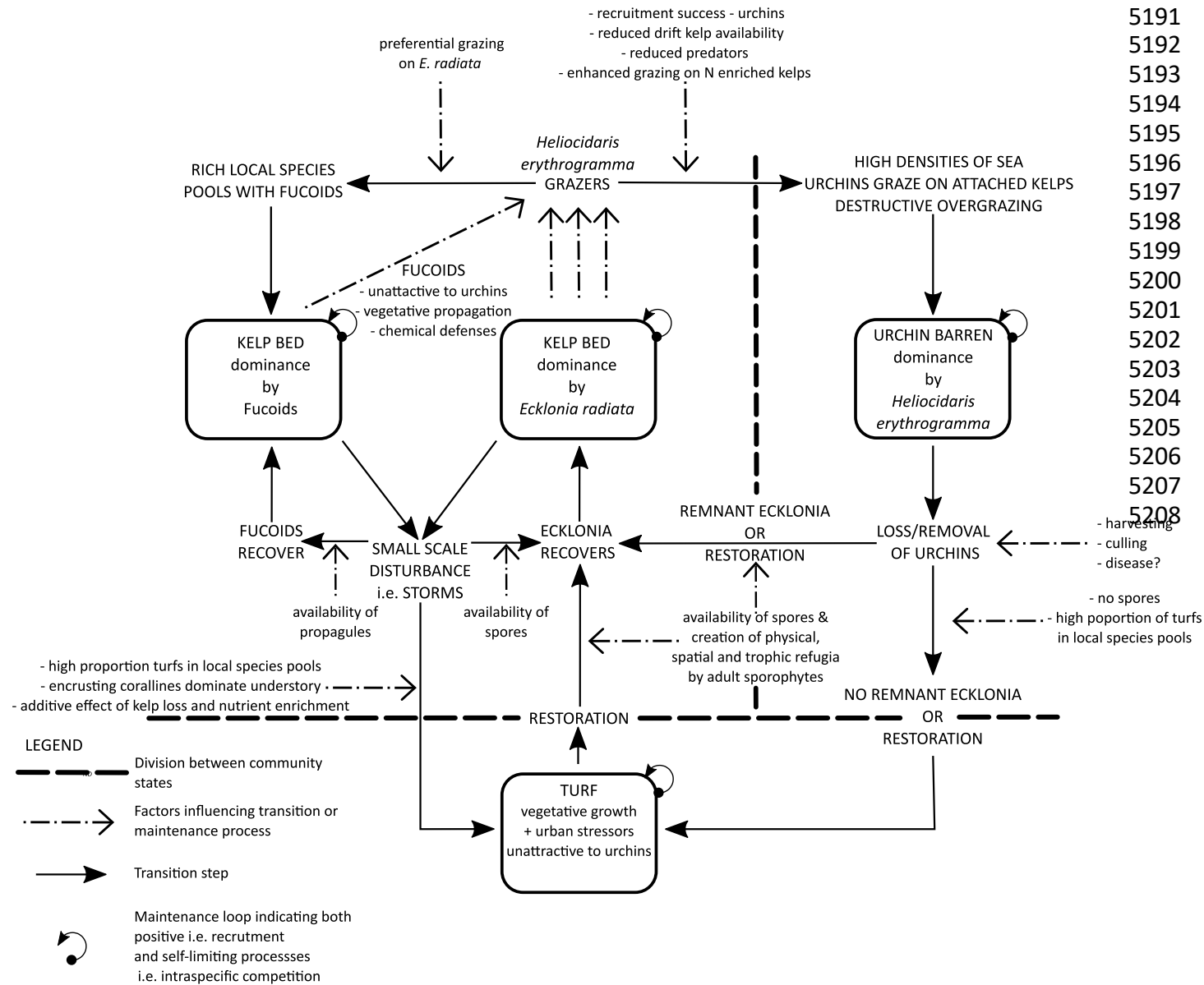


Figure 1. A qualitative model defining the mechanistic interactions among the rocky subtidal community in Port Phillip Bay. Biological disturbances trigger switches from one community state to another (i.e. urchin grazing, removal of urchins, restoration of kelps). Intrinsic biological and extrinsic environmental factors influence the likelihood of transitions between or maintenance of community states (amended from Johnson and Mann 1988; Chapman and Johnson 1990).

5209

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